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NEW SERIES, NO. 29

Revised Phylogeny and Functional Interpretation of the Edrioasteroidea Based on New Taxa from the Early and Middle Ordovician of Western Utah

Thomas E. Guensburg

James Sprinkle

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1. The forest structure, physiognomy, and floristics. *Journal of Ecology*, 51: 567-601.

Langdon, E. J. M. 1979. Yage among the Siona: Cultural patterns in visions, pp. 63-80. In Browman, D. L., and R. A. Schwarz, eds., *Spirits, Shamans, and Stars*. Mouton Publishers, The Hague, Netherlands.

Murra, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., *Handbook of South American Indians*. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

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Revised Phylogeny and Functional Interpretation of the Edrioasteroidea Based on New Taxa from the Early and Middle Ordovician of Western Utah

Thomas E. Guensburg

James Sprinkle

Abstract

Five new edrioasteroid genera from the Early and Middle Ordovician of western Utah greatly enlarge the record of this scarce echinoderm class during its early diversification. Data from a diversity of taxa were used to generate a new phylogeny and classification of the edrioasteroids. New and reinterpreted morphology, particularly for the aboral surface, is introduced. Forty-two characters were scored for 15 taxa and subjected to a PAUP 3.0 parsimony analysis. This analysis identified two major edrioasteroid clades with subsequent subbranchings. One major clade is the isorophids, whose ancestry can be traced to the Early Cambrian; the second major clade includes edrioasterids and the former class Edrioblastoidea, dating to the Middle Cambrian. Edrioblastoids, rhenopyrgids, and cyathocystids mapped as specialized branches of the edrioasterid clade, while pyrgocystinids mapped as highly derived lebetodiscid isorophids. The cladistic analysis supported our hypothesis for analogous thecal elongation structures among edrioasterids and isorophids.

The fauna contains the edrioasterid *Paredriophus elongatus*, n. gen. and sp., the edrioblastoid *Lampteroblastus hintzei*, n. gen. and sp., the agelacrinitid *Deltadiscus superbus*, n. gen. and sp., and the pyrgocystinid lebetodiscids *Archaeopyrgus anitae*, n. gen. and sp., and *Fanulodiscus crystalensis*, n. gen. and sp. Several unassigned edrioasterids are also described that provide the first information concerning edrioasterid ontogeny. All are more similar to Middle Ordovician relatives than to those of the Middle to Late Cambrian, even though the faunas are approximately equally spaced by age. The new edrioasteroids adhered to firm substrates, including hardgrounds, mounds, or bioclastic debris. *Lampteroblastus* has an elongate bud-shaped theca with short ambulacra and triangular deltoids that resemble and could be homologous with those of cyathocystid edrioasteroids. Thecal plates of *Lampteroblastus* also have heavy ridges reminiscent of certain camerate crinoids. *Archaeopyrgus*, n. gen., and *Fanulodiscus*, n. gen., provide the first detailed pyrgocystinid morphology; unique aspects of their construction include the presence of lateral hood plates and loss of ambulacral floor plates. *Deltadiscus* has extremely narrow ambulacra and a short elongation zone.

Introduction

Edrioasteroids are sparsely and sporadically distributed throughout their stratigraphic range. Fewer than 60 genera are known worldwide, even though their history spans over 300 million years, from the Early Cambrian to the Late Pennsylvanian. Such taphonomic and ecologic factors as the need for rapid, intact burial and the availability

of suitable attachment sites naturally contributed to the sparse record of these complex multielement fossils. Edrioasteroids typically inhabited firm or hard substrates, where they lived in concentrations of many individuals representing just one to a few species (see Bell, 1980; Kammer et al., 1987; Meyer, 1990; Smith, 1983; others). These would seem to be best viewed as low-diversity survival strategies (Sprinkle & Bell, 1978).

Edrioasteroids were among the first echinoderms to have diversified during the Early Cambrian metazoan radiation. The earliest taxa have been cited as the stem group to extant classes, particularly the asterozoans (Bather, 1915b; Paul & Smith, 1984; Smith, 1984, 1988; Smith & Jell, 1990), as well as lying near the base of both blastozoan and later edrioasteroid radiations (Derstler, 1981; Paul & Smith, 1984). Unlike the fossil record of most other Paleozoic echinoderms, the edrioasteroid fossil record includes a variety of Cambrian as well as later Paleozoic taxa.

Knowledge of edrioasteroids has advanced considerably in recent years, and the contributions of Bruce Bell and Andrew Smith are most significant. Bell (1976a) published the definitive monograph on North American edrioasteroids that for the first time clarified many features of internal and external skeletal construction and implemented consistent morphologic terminology. Revised descriptions and exhaustive systematics are provided for most Middle to Late Paleozoic isorophids and edrioasterids. Bell (1976a,b) also contributed substantially to our understanding of edrioasteroid ontogeny and its bearing on phylogeny. The works of Smith and co-authors (Paul & Smith, 1984; Smith, 1984, 1985, 1988; Smith & Arbizu, 1987; Smith & Jell, 1990) in many ways complement those of Bell, stressing (although not limited to) Cambrian genera and lesser-known edrioasteroid groups. These studies also include the first cladistic treatment of all major clades within the edrioasteroids and discussions of their relationships to other echinoderms. Although we disagree with some findings, these publications established a basis for comparisons with our analyses.

We describe five new genera and species of edrioasteroids from Early to Middle Ordovician rocks from the classic Ibex area of western Utah. Four named species and two undesigned taxa are from the Early Ordovician and represent the first large collection of edrioasteroids of this age. They represent the hard-won products of field work conducted over four summers by the authors and their assistants. A Middle Ordovician occurrence was discovered by a field party from Brigham Young University while measuring a section in the area. In addition to formal descriptions, excellent in-place preservation of the fossils has enabled detailed life mode and paleoecologic assessments. Widely divergent clades within the edrioasteroids are represented in the Ibex fauna, including one isorophid, multiple edrioasterids, two pyrgocystids, and one edrioblastoid. This relatively diverse

assemblage from an underrepresented part of the section served as an impetus for a revised comprehensive phylogeny of the class Edrioasteroidea based on cladistic analysis and reinterpretation of functional morphology.

We collected edrioasteroids from several localities on or more commonly near published stratigraphic sections (see Hintze, 1973). Close correlation to measured sections was usually possible by sighting along strike using a Brunton compass. Good exposure with distinctive beds, low-angle dips, and few faults made this process relatively easy. In some cases where exposure was discontinuous, correlations were checked by measuring up- or down-section to distinctive stratigraphic horizons and by noting associated fossils. Detailed facies, stratigraphic, and locality data accompany each taxon described below.

Specimens described here are deposited in the type collection at the Field Museum of Natural History (FMNH), Chicago, Illinois, indicated by the prefix PE, and in the United States National Museum, Washington, D.C., indicated by the prefix USNM. These specimens were prepared for study by cleaning with needles under a binocular microscope, and then were photographed with a thin coating of ammonium chloride sublimate, or under water.

Geologic and Stratigraphic Setting and Paleoenvironments

The Ibex area is approximately 97 km (60 mi) southwest of the town of Delta, Millard County, Utah, in the eastern portion of the Great Basin. Lower Paleozoic rocks are superbly exposed there in the House and Confusion ranges. The Lower to Middle Ordovician section is a thick depositional sequence of fossiliferous shallow-water carbonates and shales. An excellent stratigraphic and biostratigraphic framework has been established by Hintze (1951, 1952, 1973, 1987), Braithwaite (1976), Ethington and Clark (1981), Ross et al. (1982), Ross and Ethington (1991), and others. Conodont and trilobite zonations have proved most useful for age correlation with strata beyond the Ibex area. Associated biostratigraphically important zonations are reported with occurrence information below. Nearly all of the edrioasteroids were collected from four horizons in the Lower

Ordovician Fillmore Formation (see Sprinkle & Guensburg, 1993). This unit is wholly contained within the Ibexian Series, and it correlates with the Late Tremadocian through the Middle Arenig stages of British usage (Hintze, 1973, 1979). One edrioasteroid species occurs in the overlying Lehman Formation of the Whiterockian Series, and it correlates with the Llanvirnian Stage of Britain (see Ross & Ethington, 1991).

The Fillmore Formation is a 550-m-thick sequence of limestones and lesser amounts of shales interpreted to have formed on a shallow tropical ramp of the Cordilleran passive margin (Hintze, 1973; Ross et al., 1991). It has been subdivided into six informal lithostratigraphic members, each characterized by a distinctive weathering style (Hintze, 1973). Clear cyclical stacking of lithofacies is present in this section (Hintze, 1973; Datillo, 1993; pers. obs.). Most Fillmore edrioasteroids occur in close association with coarse-grained limestones and sponge-algal mounds, both of which accumulated in shallow agitated water (Church, 1974; Datillo, 1993). Coarse-grained strata include well-sorted grainstones, often developed into megaripples, and abundant intraformational conglomerates; both are interpreted to have been storm-generated (Datillo, 1993; Guensburg & Sprinkle, 1992). Pyrgocystinids were associated with fine-grained bioclastic limestones (wackestones) except for one specimen found on an intraformational conglomerate. In several cases, edrioasteroids remain attached to firm or hard substrates such as hardgrounds (former lithified seafloors) developed on the grainstones, intraformational conglomerates, or mounds, or to bioclasts such as cephalopod conchs that lay on soft, fine-grained seafloors.

The Lehman Formation is an approximately 65-m-thick sequence of limestone together with lesser amounts of quartzarenite (Hintze, 1973). This unit was not specifically studied by us; however, the single edrioasteroid-bearing slab from this unit provided to us for study is an intraformational conglomerate. The attachment mode of the edrioasteroids and staining of the slab surface indicate that this was also a hardground. Detailed descriptions of occurrences are provided for each taxon described below.

Attachment of these edrioasteroids to firm or hard substrates typifies the class as a whole. Diversification of edrioasteroids and other echinoderms during the Early Ordovician has been attributed to the widespread availability of habitable sites (Guensburg & Sprinkle, 1992).

Edrioasteroid Phylogeny

This revised phylogeny of the edrioasteroids contains a cladistic analysis with discussion. Conclusions differ from those of previous authors primarily in (a) the placement of pyrgocystinids, for which we also introduce new morphologic terminology, and (b) the interpretation of homology and analogy for the aboral surface and thecal elongation morphology. Differing usages of terminology among various authors complicate the second point, and we provide clarification where needed. We discuss several smaller points of contention regarding other aspects of edrioasteroid morphology, as well. We include in this study only those groups traditionally assigned to edrioasteroids and edrioblastoids. Among the data is the first comprehensive set for pyrgocystinids.

Relationships of the edrioblastoids to other echinoderm classes have long been debated. Basler (1935) classified them as a family within the edrioasteroids, but other workers hypothesized a closer relationship to blastoids (Fay, 1962; Hudson, 1925; others). Fay (1962) elevated the then-monospecific clade to class level, comparing them to both edrioasteroids and blastoids. Recently, Smith and Jell (1990) described an early edrioblastoid that provided much new morphologic evidence linking edrioblastoids with edrioasteroids. Our findings further support this relationship.

We have not included cyclocystoids or asterozoans in the parsimony analysis even though in the past they were presented as having been derived from edrioasteroids (Bather, 1915b; Guensburg, 1988; Paul & Smith, 1984; Smith, 1985; Smith & Jell, 1990; others). The relationship of either group to edrioasteroids is obscure and hampered by the lack of clearly diagnostic fossils. Arguments pro and con have been set forth in previous works, and the fossils described here provide no additional evidence (see Blake, 1994; Blake & Guensburg, 1993; Guensburg, 1988; Smith, 1985; Smith & Jell, 1990).

This parsimony analysis includes data from 15 taxa that we feel sample a wide morphologic and taxonomic diversity of the class (Fig. 1). Characters were selected based on a thorough review of edrioasteroid morphology, and all portions of the theca were included. We have attempted to code characters conservatively and avoid general features that could readily be subject to convergence, such as thecal shape. Several nested or uninformative characters were deleted during trial runs. Reasonably complete data sets were available, ex-

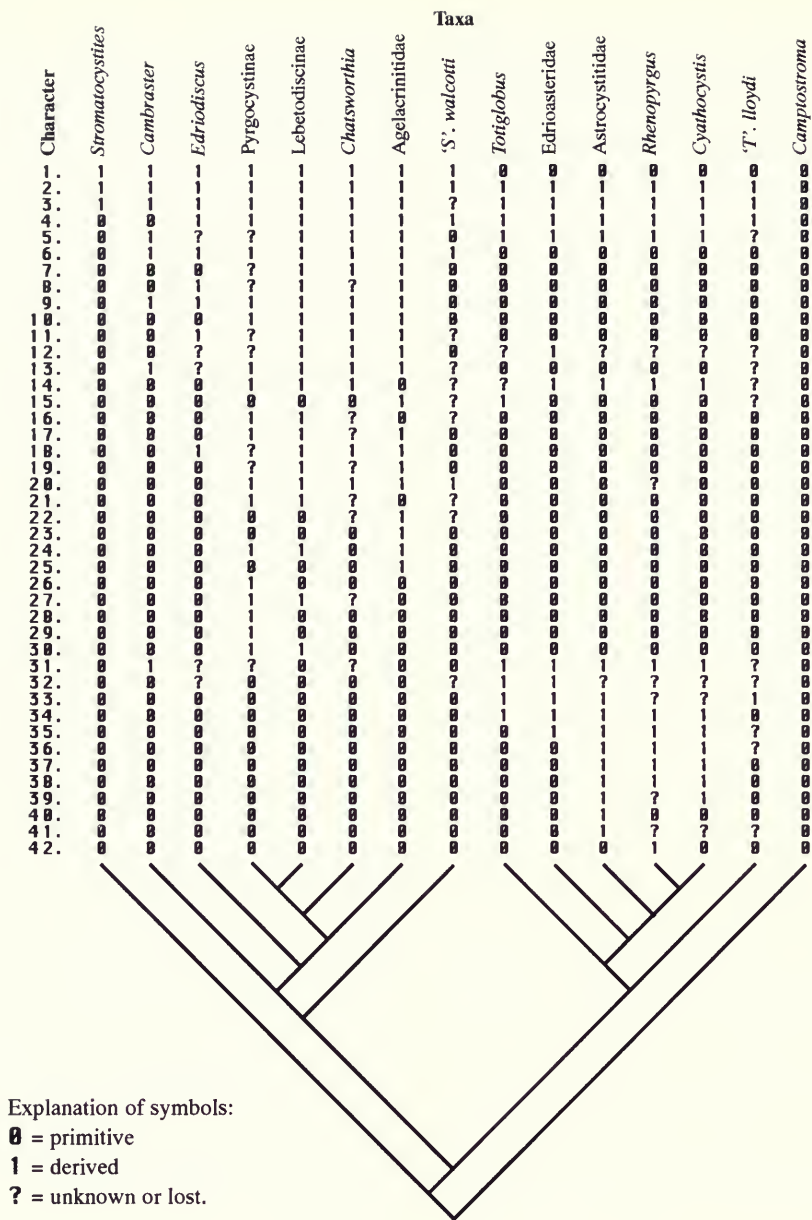


FIG. 1. Data matrix for the edriasteroid parsimony analysis. Explanation of the characters along with polarities is provided in Table 1. One of the two preferred maximum parsimony trees is included below for comparison.

cept for those of a few Cambrian taxa (Fig. 1). They constitute the best current information for early edriasteroid morphology. Forty-two characters were polarized and assembled into a data matrix (Table 1); these data were then subjected to a maximum parsimony analysis using PAUP version 3.0n (Swofford, 1991). Characters were

unweighted. Eighteen most-parsimonious trees of 54 steps were obtained using a branch-and-bound search, which guarantees maximum parsimony tree discovery. Consistency indices (CIs) for the trees were 0.778 with uninformative characters included and 0.721 with uninformative characters deleted. The skewness measure (g_1) of the tree length

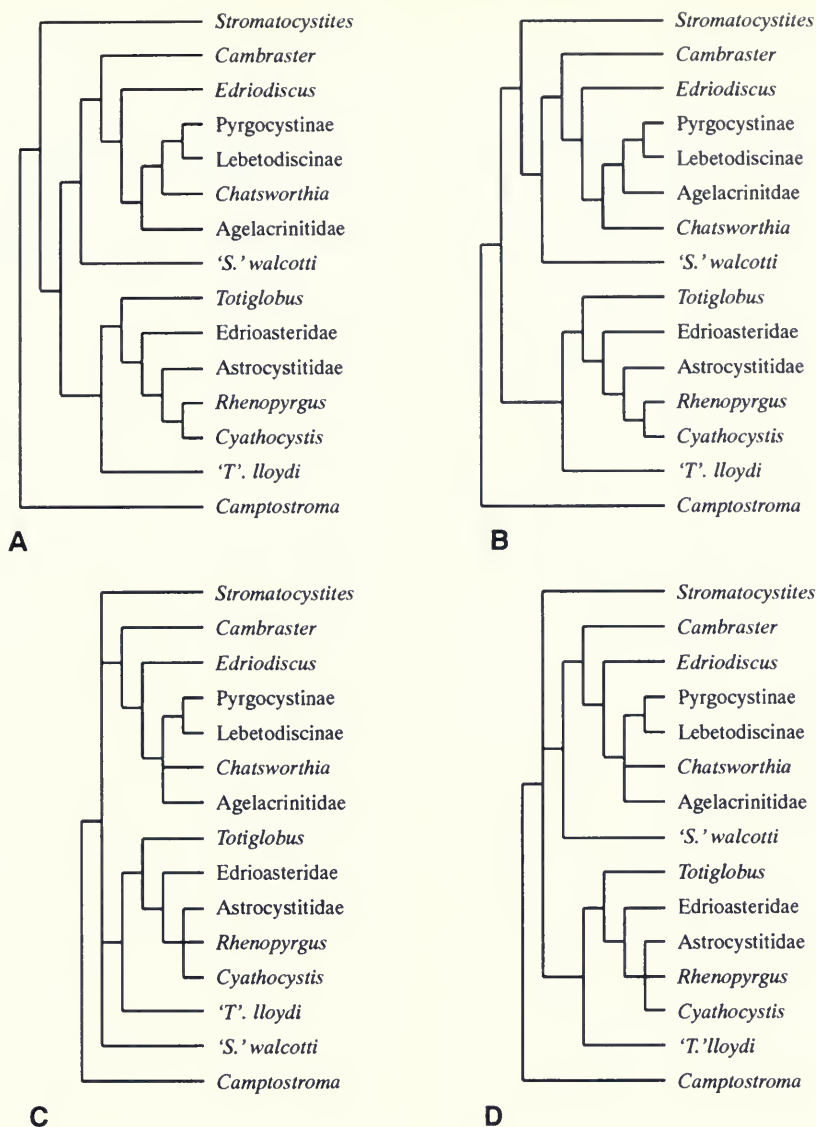


FIG. 2. Cladograms generated by the edrioasteroid parsimony analysis. **A, B**, Two preferred trees; **C, D**, Adams and strict consensus trees, respectively.

distribution was -1.01 , indicating a high level of phylogenetic signal (Huelsenbeck, 1991). We illustrate two preferred trees along with Adams and strict consensus trees (Fig. 2), and one preferred tree is combined with the data matrix for comparison (Fig. 1). The consensus trees each contain three polytomies at similar locations where data are sparse. Stratigraphic occurrences of the taxa agree well with the preferred trees.

Like Paul and Smith (1984), we use *Camptostro-*

ma of the Early Cambrian as the outgroup for edrioasteroid parsimony. Derstler (1981) and Paul and Smith (1984) reinterpreted the morphology and phylogenetic position of *Camptostroma* in slightly different ways. Both restored the oral surface with the basic edrioasteroid morphology, including an upward-oriented domal surface incorporating five ambulacra arrayed in a 2–1–2 pattern and lacking skeletized appendages, a central mouth with unfused mouth frame, food grooves with bi-

TABLE 1. Characters used in the cladistic analysis of edrioasteroids.

Derived	Primitive
1. Attachment surface expanded beyond basal disc	Attachment surface a basal disc
2. Thecal plating unilaminar	Thecal plating multilaminar
3. Primary cover plates	Primary cover plates lacking
4. Epispires lacking	Epispires present
5. Oral frame of compound plates	Frame plates not fused
6. Marginal ring	Marginal ring lacking
7. Basal disc decalcified	Basal disc plated
8. Aboral ribbing	Ribbing lacking
9. Peripheral rim	Rim lacking
10. Interambulacra imbricate	Interambulacra tesellate
11. Floor plates hidden	Floor plates exposed
12. Oral frame with five compound radial plates	Compound radial orals lacking
13. Hydropore slit with hydropore oral plate	Hydropore a pore bounded by several interambulacra
14. Cover plates a uniform biseries	Cover plates an irregular biseries
15. Cover plates a uniform triseries or greater	Cover plates an irregular multiseries
16. Intrathecal cover plate passageways	Passageways lacking
17. Intrathecal cover plate extensions	Extensions lacking
18. Trough-shaped food groove	Notched food groove
19. Uniserial floor plates	Biserial floor plates
20. Sutural passageways lacking	Sutural passageways
21. Three primary differentiated oral cover plates	Oral cover plates nondifferentiated
22. Four or more primary differentiated oral cover plates	Oral cover plates nondifferentiated
23. Valvular periproct of uniform wedge-shaped plates	Periproct with irregular platelets
24. Pedunculate zone	Pedunculate zone lacking
25. Recumbent zone	Recumbent zone lacking
26. Floor plates lacking	Floor plates
27. Prismatic cover plates	Tabular cover plates
28. Hood plates	Hood plates lacking
29. Articulated spines	Spines lacking
30. Petaloid ambulacra	Ambulacra straight-sided or with distal taper
31. Oral frame with five compound interradial plates	Compound interradial plates lacking

TABLE 1. Continued.

Derived	Primitive
32. Hydropore a fixed pore or slit, shared across two interambulacra	Hydropore a pore bounded by several interambulacra
33. Ambulacra with broad lateral floor plate extensions	Broad lateral floor plate extensions lacking
34. Basal disc plate ring above substrate	Plate ring contacting substrate
35. Collar	Collar lacking
36. All interradial cover plates meet over mouth	Lateral interradial plates separated from others
37. Deltoids	Deltoids lacking
38. Hydropore lost or fixed pore through deltoid	Hydropore a pore bounded by several interambulacra
39. Sutural passageways small, shifted abradially	Passageways relatively large adradial
40. Interambulacra in uniform circlelets	Interambulacra irregular
41. Stalk with plate mosaic or columniform plates	Stalk lacking
42. Coriaceous sac	Sac lacking

serial laterally exposed floor plates with sutural pores below, articulating cover plate sheets above, and hydropore and periproct in a broad CD interray. However, Paul and Smith (1984, Fig. 5) depicted *Camptostroma* with a wide conical aboral surface that was unattached and presumably inserted into soft substrata. In this respect, *Camptostroma* would have been more like helicoplacoids, from earlier in the Cambrian. This is consistent with the hypothesis of these authors that *Camptostroma* was the stem group to all other pentaradiate echinoderms. Derstler (1981) considered *Camptostroma* to be an edrioasteroid not far removed from the ancestry of blastozoan echinoderms. He illustrated the aboral surface of *Camptostroma* with a convex zone surrounding a flat central platform (Derstler, 1981, Fig. 1). (See Durham, 1967, Fig. 396, for an excellent illustration of a specimen showing this feature.) We examined specimens in our possession and believe the Derstler restoration to be accurate. We interpret the central platform to be the basal disc (see Function and Evolution, below) generally like that of other early edrioasteroids, further reinforcing the view that *Camptostroma* was an edrioasteroid. The term basal disc was used by Bell and Sprinkle

(1978) for the attachment structure of *Totiglobus*, and we apply this term universally to edrioasteroid aboral structures capable of maintaining suction for clinging.

Two initial branching patterns were generated by the parsimony analysis (Fig. 1). In some trees, *Stromatocystites* of the Early to Middle Cambrian was the sister group to *Camptostroma*. An analysis by Smith (1985) produced similar findings. *Stromatocystites* was the stem taxon of the isorophid edrioasteroids in other trees. The discoidal theca of this taxon is reminiscent of isorophids. The oral surface of *Stromatocystites* is much like that of *Camptostroma*, but the aboral surface is broad and flat (Smith, 1985; Smith & Jell, 1990). The basal disc has a plate ring inside (aboral to) the thecal margin. In our opinion, other workers have mistaken this structure for the marginal ring in certain derived taxa (for instance in Bell, 1980; Smith, 1985; Smith & Jell, 1990) (see below). Internally, the basal disc of *S. reduncus* is distinguished by a series of ridges radiating outward from the plate ring (Smith & Jell, 1990).

The parsimony analysis supports observations of Smith and Jell (1990, pp. 726–727), who regarded “*Stromatocystites*” *walcotti* as having isorophid synapomorphies. This taxon represents a new genus, but its redescription would require much further study, so we refer to it as “*S.*” *walcotti*. It has an ill-defined marginal ring bordering the lateral thecal margin (Smith, 1985, text Figs. 4, 7) and the aboral surface had a basal disc with plate ring, providing evidence that these two structures are separate and independently derived. The plate ring is the older and more widely distributed of the two. The floor plates, although biserially plated, have a narrow trough shape and lack sutural pores; these are both isorophid synapomorphies (Fig. 3). The main body of these plates is adradial and proximodistally elongate. Each floor plate commonly bears two (sometimes one) lateral projections that articulate with similar projections from interambulacral plates.

Cambraster plotted as the sister group to “*S.*” *walcotti* (Figs. 1, 2). It is a problematic fossil from the Middle Cambrian (Fig. 1) (Smith, 1985; Jell et al., 1985). Biserial floor plates, sutural pores, and full aboral plating are plesiomorphous. A basal disc with plate ring is present. There is a large marginal ring and a peripheral rim forming the thecal margin. This, together with the presence of an articulated hydropore plate, are isorophid synapomorphies. The oral frame consists of five interradially positioned elements that appear to be

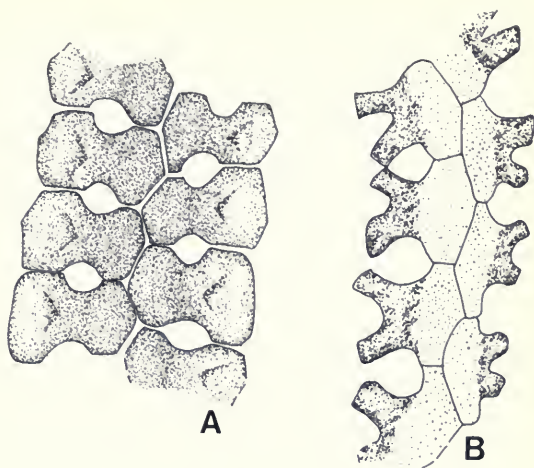


FIG. 3. Comparison of floor plate arrangement and morphology between *Stromatocystites pentangularis* and “*S.*” *walcotti*. **A**, Reconstructed floor plate series of *S. pentangularis* in exterior oral view based on drawings of individual floor plates in Smith (1985, text Fig. 6); cover plates with sutural passageways typical of primitive edrioasteroids and edrioasterids, much enlarged. **B**, Floor plate series of “*S.*” *walcotti* in interior oral view taken from USNM 376690 and modified from Smith (1985, text Fig. 7); floor plates elongated with lateral prongs, no sutural passageways.

apomorphous because radially positioned plates form the oral frame of typical isorophids.

Edriodiscus, also of the Middle Cambrian, plotted as the sister group to *Cambraster* in the parsimony analysis. Its morphology is incompletely known but appears to have been intermediate between that of “*S.*” *walcotti* and typical isorophids (see Smith, 1985, text Fig. 12, for a similar finding). Synapomorphies with typical isorophids include a marginal plate ring with uniserial plate circlets beyond forming the thecal margin, aboral ribbing, and trough-shaped floor plates. Plesiomorphies with *Stromatocystites* include a fully plated aboral surface, calcified basal disc with plate ring, and perhaps biserial floor plates.

Smith and Jell (1990, p. 771 and Fig. 51) generated a phylogenetic analysis in which *Edriodiscus*, *Cambraster*, and “*S.*” *walcotti* mapped as branching toward ancestral sea stars prior to the edrioasterid–isorophid dichotomy. Few synapomorphies among these three taxa and traditional isorophids were discovered by their analysis. We feel their results were spurious, for the following reasons. Only 16 characters were provided in the full analysis. Oral surface convexity (their character 7) and ambulacral curvature (character 4) are

not significant at high phylogenetic level. For instance, we use convexity as a generic taxobasis to separate the edriosterids *Paredriophus* and *Edriophus*, genera that numerous synapomorphies suggest were closely related. Smith and Jell (1990, p. 720) themselves applied ambulacral curvature as a specific taxobasis for *Stromatocystites*. Finally, the hypotheses for homology of some morphologies used by Smith and Jell cannot be substantiated, and in our opinion these authors did not provide a balanced treatment of the evidence. They homologized the marginal ring of *Edriodiscus* with marginals of the early sea star *Archaeogonaster* and applied this hypothesis (characters 12 and 15) to their cladogram (Smith & Jell, 1990, Table D) (see Blake & Guensburg, 1993; Blake, 1994, for critiques). In conjunction, they expressed doubt as to the homology of marginal ring plates with the proximal circlet of the peripheral rim of typical isorophids. They contrasted the two, stating that the marginal ring plates of *Edriodiscus* were “stout barrel-shaped ossicles that abut” whereas those of isorophids were “thin imbricate plates that overlap” (Smith & Jell, 1990, p. 771). However, much evidence supporting the case for homology was not discussed. The marginal ring of *Edriodiscus* contacts the theca below and bounds the thecal margin in exactly the same manner as the proximal circlet, and there is aboral ribbing in both cases. The isorophids *Savagella* and *Hystri-chopsydrex* have abutting proximal circlet plates similar in size to those of *Edriodiscus* (Guensburg, 1988), and the imbricate proximal circlet of typical isorophids is usually not thin but thick. Smith (1985, p. 729, 753) previously recognized the similarities between the peripheral rims of *Savagella* and *Edriodiscus* and the aboral ribbing of agelacrinid isorophids and *Edriodiscus*.

The Late Cambrian *Chatsworthia* is poorly known but appears to have achieved the typical isorophid design that persisted for much of the remainder of the Paleozoic (Smith & Jell, 1990) (Fig. 1). The theca is discoidal and the marginal ring consists of imbricate plates integrated into the peripheral rim as the proximal circlet. Central aboral plating is apparently lacking, and we presume the basal disc was decalcified. Cover plating included uniform primary plates, and floor plates are entirely internal. The branching order of *Chatsworthia*, lebetodiscinids, and agelacrinids was unresolved by the parsimony analysis (Fig. 2). The various trees depict *Chatsworthia* as the sister group to all post-Cambrian isorophids or as the sister group to lebetodiscids. Details of the oral area and

ambulacral construction for *Chatsworthia*, if known, would likely resolve this uncertainty. Lebetodiscid and agelacrinid isorophids were the most diverse and long-ranging edriosteroids. They are distinguished by details of the ambulacra, oral plating, and periproct (Fig. 1) (see also Bell, 1976a, 1980, for thorough discussions). Oral cover plates of both groups are distinct from ambulacral cover plating and included articulated hydropore plates. Ambulacral cover plates of agelacrinids often form a complex uniform multiseriis, and there is a valvular periproct with distinctive uniform plating (Bell, 1976a). Pyrgocystinids plotted as the sister group to the lebetodiscinids in the parsimony analysis (Figs. 1, 2). (See Kesling, 1967, p. 201, and Bell, 1980, pp. 160, 165, for supportive statements.) They have unique ambulacral construction among edriosteroids in which the floor plates are lost and hood plates are present (see pyrgocystinid discussion under Systematic Paleontology).

The clearest evidence for the origin of thecal elongation structures in edriosteroids is the pedunculate zone found in two isorophid clades, pyrgocystinid lebetodiscids and clavate agelacrinids. Elongation was achieved in both cases by the addition of plates from the interambulacra that extend the theca beyond the ambulacra, but proximal to the peripheral rim (including the marginal ring). In pyrgocystinids, the pedunculate zone is cylindrical and composed of squamose plates similar to interambulacra. In clavate agelacrinids, there is further elaboration with a distinctive recumbent zone proximal to well-ordered columns of squamose plates of the pedunculate zone (Sumrall, 1992). The pedunculate zone of both pyrgocystinid lebetodiscids and clavate agelacrinids does not frame the theca but bounds the basal attachment area beneath the theca. Several examples of incipient thecal elongation are also found in isorophids (*Cystaster*, *Stalticodiscus*, *Ulrichidiscus*, and *Deltadiscus*; see also Sumrall & Sprinkle [1990]), and therefore it is a subjective matter as to what qualifies as a pedunculate zone.

The parsimony analysis mapped edriosterids, edrioblastoids, and cyathocystids (Figs. 1, 2) as a sister group to the isorophids. These taxa had globular, clavate, bud-shaped, and cylindrical thecae (see Sprinkle & Bell, 1978; Bell, 1982; Smith, 1985). They retained plesiomorphic ambulacra with laterally exposed floor plates and sutural passageways, although the floor plates were fused, forming deltoids in some species. The parsimony analysis supports our assertion that the peripheral rim and

marginal ring were lacking in this clade (Fig. 1). "*Totiglobus*" *lloydi* and *Totiglobus*, both Middle Cambrian, were early branches (Figs. 1, 2). *Totiglobus* is particularly well known. The aboral surface has a small basal disc bordered by a plate ring (termed "marginal plates" by Bell & Sprinkle, 1978, p. 254, and "marginal ring" by Smith, 1985) bearing internal septate radiating ridges. Ridges converge from the plate ring toward the center of the basal disc (there is no smooth central platform as found in *Stromatocystites reduncus*; see above) (Bell & Sprinkle, 1978, text Fig. 4). The broad ambulacra are arranged in the plesiomorphic 2–1–2 pattern but are roofed by derived uniform biserial cover plates. Oral cover plates, in contrast to those in isorophids, are not differentiated from ambulacral cover plates. "*Totiglobus*" *lloydi* was provisionally assigned to genus at the time of its description because of poor preservation (Sprinkle, 1985). The theca is bud-shaped, and the oral surface appears to be similar to *Totiglobus*, but there is a short conical tessellate-plated elongation of the theca distal to the ambulacra. The basal disc is unknown. *Walcottidiscus* from the Middle Cambrian has been presented as the sister group to the edrioasterids (Smith & Jell, 1990, p. 771). The specimens are all poorly preserved and lack most data, so we omitted this taxon from the parsimony analysis. There appear to have been imbricate plate circlets distal to the ambulacral tips and surrounding a noncalcified central area (see Smith, 1985, Pl. 89), vaguely similar to a plate collar (see below).

The edrioasterids branched as the sister group to *Totiglobus* in the parsimony analysis (see Paul & Smith, 1984, p. 468, for a supportive view). Along with those features of the oral surface mentioned above for *Totiglobus*, edrioasterids have a fixed hydropore slit through the interambulacral plates. The distal theca has a short, stalk-like collar of small, partly imbricate plates or platelets (Bell, 1976a). The collar joins the theca abruptly at a flange (part of the "resting zone" of Bell, 1976a). We interpret flange plates as probably homologous to the basal disc plate ring; the collar would then have been derived from the basal disc. Less likely, both collar and plate ring were derived by modification of the theca between the ambulacra and the basal disc. Whichever case is correct, this construction differs from isorophids, in which the marginal ring/peripheral rim contacts the substrate beyond the basal disc and the elongate pedunculate zone, if present, is above.

Cyathocystids and edrioblastoids branched from edrioasterids, but their interrelationships were un-

resolved by the parsimony analysis (Fig. 1). Synapomorphies linking these two disparate groups and typical edrioasterids are a globular or elongated theca, typically with tessellate plating; a fixed hydropore (not bordered by articulated plates); broad ambulacra elevated by inclined lateral floor plate extensions; nonporous uniform biserial cover plates (edrioasterids such as *Edrioaster* have tiny accessory plates along the perradial suture); and a basal disc plate ring and collar or stalk.

Bell (1980, p. 169) commented that edrioblastoids and cyathocystids share similarities of construction, and they were linked as sister groups in a parsimony analysis by Smith and Jell (1990, p. 745). These authors acknowledged the tenuous connection resulting from the great morphologic disparity among the few known taxa. The cladistic analysis, including data from new taxa, produced similar findings (Figs. 1, 2). The most convincing synapomorphies are the oral cover plate arrangement and the nature of the floor plates. Both cyathocystids and edrioblastoids have five elongate oral cover plates ("primordial orals" of Smith, 1985; Smith & Jell, 1990) occupying the interradian position and meeting centrally above the mouth. There is, in effect, a nearly pentaradial symmetry in both groups. This arrangement differs from edrioasterids in that the lateral interradian cover plates ("lateral bifurcation plates" of Bell, 1976a) are not separated from the other three interradian cover plates. The floor plates in both cases consist of deltoids, each of which is formed of adjacent half ambulacra pairs bordering interambulacra. Bell (1982) and Bockelie and Paul (1983) interpreted the deltoids in cyathocystids as being interambulacral or interradian (and both therefore also concluded that cyathocystids lacked floor plates), whereas Smith and Jell (1990) argued that they were modified floor plates homologous with those of edrioblastoids. We agree with Smith and Jell because the deltoids in cyathocystids, despite their expanded size and lateral position, still support and articulate with the cover plates in the usual manner found in almost all other edrioasteroids. The deltoids of the Early Ordovician edrioblastoid *Lampteroblastus* described here are reminiscent of those in cyathocystids. They are triangular, level with adjacent interambulacral thecal plates, and fill the interambulacra.

Smith and Jell (1990, pp. 745–746) stated that the deltoid plates of the advanced edrioblastoid *Astrocystites* represent the expanded "first ambulacral flooring plates," therefore implying the elimination of all other flooring plates. These authors

did not suggest how this could have occurred in relation to other features, such as the deltoid pore system, or the effects on the overlying cover plates, and they cited no intermediates to support their case. We hypothesize that deltoids formed by fusion of all the floor plates from two adjacent ambulacra and the connecting oral frame plate. In support of our interpretation, we note that (a) there is no loss of contact between existing floor plates and cover plates or wholesale shifting of contacts as would be required in the expanded flooring plate scenario; (b) the system of through-going pores of each deltoid in edrioblastoids and cyathocystids consists of reduced sutural pores analogous to those of other edrioasterids (one of us [T.E.G.] has recently collected a specimen of *Cyathocystis* that preserves sutural pores like those found in edrioblastoids such as *Astrocystites* [Fig. 17D]); (c) the distal floor plates taper with diminishing abradial exposure, which would produce a shape similar to deltoids if fused; and (d) fusion of floor plates, at least around the oral area, was a universal feature among all but the most primitive edrioasteroids and therefore is consistent with other clades.

Suggested homologies for the aboral morphologies of the cyathocystid *Rhenopyrgus* and the edrioblastoids *Cambroblastus* and *Astrocystites* were provided by Smith and Jell (1990, text Fig. 34). We accept this interpretation as a strong possibility, but we believe different terminology should be used: plate ring rather than “marginal” zone, again reflecting our finding that marginal ring plates are found only in isorophids. Smith and Jell (1990, p. 745) interpreted the Late Cambrian edrioblastoid *Cambroblastus* as too specialized to have been a suitable ancestor to cyathocystids because of derived features, including the narrow stalk and standardization of thecal plates into distinct circlets. On the other hand, *Cambroblastus* has no deltoids (Smith & Jell, 1990, p. 749), a critical synapomorphy with cyathocystids; instead, it apparently has plesiomorphous biserial floor plates. The Early Ordovician *Lampteroblastus*, n. gen., has triangular deltoids without raised margins, very reminiscent of the deltoids found in cyathocystids, but the lower theca and stalk morphologies are of typical edrioblastoid construction.

Aboral and elongation structures of cyathocystids are unique among edrioasteroids: a solid fused cuplike element of *Cyathocystis* or distal imbricate zone and coriaceous sac of *Rhenopyrgus*. These are so different that we use them as a subfamilial taxobasis within the Cyathocystidae. Both could have

evolved by extensive modification of the basal disc, but there are as yet no fossils providing intermediate morphologies. Features of the ambulacra/oral area and intrambulacra for the two genera are remarkably similar. *Rhenopyrgus grayae* and *Cyathocystis* spp. have a plate ring surrounding the oral area proximal to the distal fused cup. Bockelie and Paul (1983, Fig. 4) homologized these structures with the “marginal ring” or “pedunculate zone” of isorophids, but this is incorrect in our opinion. The situation of cyathocystids is like that of edrioasterids, where a plate ring is followed by the elongation structure (collar or cup).

Considering edrioblastoids separately, we believe they were the sister group to edrioasterids, whose origin can perhaps be traced back through *Cambroblastus* to the Middle Cambrian “*Totiglobus*” *lloydi*. *Cambroblastus* (Smith & Jell, 1990), with its much elongated polyplated stalk or short ambulacra with persistently plesiomorphic biserial floor plates, is a morphologic intermediate between “*T.*” *lloydi* and the Ordovician *Lampteroblastus* and *Astrocystites*. The stalk and theca of the latter two advanced edrioblastoids presumably evolved through the plate reduction and uniformity that typified many lineages after the Cambrian (Guensburg & Sprinkle, 1992). The theca of edrioblastoids is remarkably convergent with the theca of parabalastoids and blastoids. The edrioblastoid stalk appears to have evolved through a series of steps similar to that of blastozoans and crinoids (see Paul & Smith, 1984, Fig. 15).

Function and Evolution

Previous authors generally agree that edrioasteroids were sessile low-level suspension-feeding organisms (Bell, 1976a; Smith, 1985; Sumrall & Sprinkle, 1992; others). Psolid holothurians (Regnéll, 1966; Derstler, 1985; Guensburg, 1988) and balanimorph barnacles (Sumrall & Sprinkle, 1992) have been suggested as general modern analogues for isorophid edrioasteroids. Details must be reconstructed from morphologies and associated paleoenvironments, and contention over aspects of edrioasteroid paleobiology remains. The following discussion outlines temporal changes in the functional morphology of feeding, respiration, positioning, and posturing for edrioasteroids.

Edrioasteroids were presumably ciliated mucus feeders (Smith, 1985, p. 727). If so, cilia likely

covered the epithelial lining of the ambulacral tunnels, creating feeding currents and transporting food particles along a mucous train to the mouth. Most Early and Middle Cambrian and later edrioasterid edrioasteroids had sutural pores through the floor plates that presumably housed ducts leading to internal ampullae (Bell, 1976a; Smith, 1985). This suggests the presence of extensible tube feet that could have supplemented food gathering or provided a mechanism to open the cover plates (Smith, 1985, pp. 726–727). Competing interpretations depict the radial canal as either external (Bather, 1915a; Paul & Smith, 1984; Smith, 1985) or internal beneath the floor plates (Bell, 1976a). We prefer the former interpretation for the reasons given by Smith (1985, p. 725, text Fig. 8) and the fact that there is a secondary groove along the perradial suture in edrioasterids such as *Edriophus* that could have held the radial canal (see Bell, 1976, text Fig. 2B). As pointed out by Smith (1985, p. 725), the ambulacral construction of isorophids is highly derived. Sutural pores have been lost, and the floor plates form a smooth trough along the base of the ambulacra. We cannot identify any specific structures that housed ampullae, or the radial canal, and we hypothesize that they and tube feet were lacking. If so, opening and closing the cover plates was accomplished by connective tissues, and food gathering was by the ciliated epithelial lining. Isorophid cover plates articulated with interambulacrals laterally (rather than with inclined lateral floor plates) and floor plates below (rather than floor plates only). The gap between interambulacrals and floor plates was occupied by cover plate extensions that projected into the thecal interior, presumably providing the mechanism to fully operate the cover plates without exposing the connective tissues (see Bell, 1976a, text Fig. 1B). Smaller secondary cover plates composed uniform multiseries for agelacrinitid isorophids. The most elaborate patterns of these occur in Carboniferous discocystid agelacrinitids, for which there is a complex oscillating perradial suture that can span nearly the entire ambulacral width (e.g., Sumrall, 1992). This presumably facilitated feeding with slight gaping of the cover plates (similar to the development of plications in certain articulate brachiopods), reducing exposure of the food groove. Ambulacra of discocystids were conversely very narrow.

Specialized respiratory structures were present in all edrioasteroids. Early to Middle Cambrian taxa often had epispires between interambulacrals,

and the Ordovician edrioblastoid *Astrocystites* had thin stereom and channelways at interambulacral plate corners. A hydropore is found in all edrioasteroids but appears to be more elaborate in isorophids, in which there was an articulated and often large hydropore oral plate. Edrioasterids and derivatives had a small fixed hydropore slit or pore. Respiration for agelacrinitid isorophids was apparently supplemented by anal pumping using the valvular periproct, similar to holothurians or comatulid crinoids (Williams, 1918; Bell, 1976a; Sumrall & Sprinkle, 1991). Lebetodiscid isorophids had specialized pores or thin stereom between adjacent cover plates (intrathecal passageways) (Bell, 1976a, p. 38). Additional pores are found between hood plates of pyrgocystinids (see pyrgocystinid discussion under Systematic Paleontology).

Early and Middle Cambrian edrioasteroids had fully plated aboral surfaces incorporating basal discs. The basal disc in all these taxa except *Camplostroma* was strengthened by one or sometimes two plate rings. The interior disc surface has been described in detail for *Stromatocystites reduncus* (Smith & Jell, 1990) and *Totiglobus nimius* (Bell & Sprinkle, 1978). In both species, ridges radiating from ring plates onto other disc plates presumably served as attachment sites for connective tissues and are interpreted to have enabled clinging by suction (Bell & Sprinkle, 1978; Smith, 1985; Smith & Jell, 1990). These organisms presumably released after death or when under duress, and not surprisingly, few of the fossils are preserved adhering to any recognizable surface. A *Totiglobus*-like specimen in our possession is affixed to a trilobite free cheek. Smith (1985) previously hypothesized that two of the genera, *Stromatocystites* and *Cambraster*, lay unattached on the seafloor. Yet it seems reasonable to assume that some sort of firm surface would have been necessary for suction to have been effective. Perhaps adhesion sites had low preservation potential (see Guensburg, 1988, for a similar discussion on unusual isorophid edrioasteroids). The marginal ring of the early edrioasteroids "*Stromatocystites*" *walcotti* and *Cambraster* did not contact the substrate and presumably stiffened the theca, but later this structure was incorporated into the peripheral rim of all isorophids and participated in sealing the thecal margin, as well.

Isorophid edrioasteroids beginning with the Middle Cambrian *Edriodiscus* had a uniserially plated peripheral rim contacting the substrate be-

yond the basal disc. Lower plate surfaces were radially ribbed, presumably enabling more effective gripping (Caster, in Bell, 1976a, p. 30). The basal disc area was decalcified in most taxa by the Late Cambrian. The peripheral rim, like the basal disc, was not skeletally attached, but the vast majority of isorophids are preserved adhering to hard calcareous surfaces. Sites included several types of bioclastic or mound hardgrounds and a variety of "shelly" surfaces: bivalves, cephalopods, gastropods, rugose corals, brachiopods, bryozoans, crinoids, blastozoans, and trilobites. Many fossils preserve only the peripheral rim or a partial peripheral rim, with the remainder of the theca highly disrupted or even missing. Therefore, this structure must have sealed the thecal margin with some sort of durable biochemical adhesive or tissue (Bell, 1976a).

The aboral surface of many edrioasterid edrioasteroids is not well known, but presumably they adhered by suction as well. The substrate-contacting surface of *Paredriophus* was apparently fully plated (Fig. 4D) but that of *Edrioaster* was apparently decalcified (Bell, 1976b, Pl. 58, Fig. 4). Most edrioasterids occur on hardgrounds. Cyathocystids had unusual aboral morphologies for edrioasteroids. *Cyathocystis* was skeletally cemented without a basal disc (Bockelie & Paul, 1983, p. 258). *Rhenopyrgus* presumably lived partly embedded in soft substrata, anchored by a coriaceous sac (Smith, 1985).

The evidence as to whether most edrioasteroids could move is contentious (see Bell, 1976a; Meyer, 1990; Smith, 1983; Sumrall & Sprinkle, 1992), but it would seem that adhesion by suction would have provided ample opportunity to do so. All modern organisms using this type of attachment of which we are aware, such as psoloid holothurians, polyclacophorans, limpets, and anemones, have this capability. Holdfasts of fixed echinoderms (cyathocystid edrioasteroids, some crinoids) skeletally attach to hard surfaces. Even limited movement potential for edrioasteroids could have provided versatility by enabling repositioning and reattachment.

Elongation of the theca among isorophids was accomplished by an extensible pedunculate zone of highly imbricate plates. This construction provided the means to extend the theca to advantageous feeding or gamete broadcasting levels but required an extensive supporting system of ligamentous tissues. Some pyrgocystinids and clavate agelacrinitids had exaggerated pedunculate zones

that could not have been withdrawn into the area within the peripheral rim but were still capable of considerable contraction (Sumrall, 1992, Figs. 3, 11D).

The distal collar of edrioasterids was composed of nonimbricate or only slightly imbricate plates that we hypothesize had limited contraction capabilities and therefore functioned more as a short stalk than a pedunculate zone. The stalk of edrioblastoids was presumably derived from the distal collar or interambulacra and initially consisted of a rigid plate mosaic, but was modified in more derived forms to columniform plates. Thecal elongation in *Rhenopyrgus* was accomplished with an extensible collar closely convergent on the isorophid pedunculate zone. The distal cup of *Cyathocystis* can be considerably elongated. Many *Cyathocystis* specimens recently discovered by the senior author in original position are inverted or laterally oriented in reef cavities or overhangs, similar to occurrences of the extant crinoid *Holopus*.

Revised Classification

A revised Linnaean classification of the class Edrioasteroidea is offered below. The extensive new material described here has reinforced our belief that edrioasteroid clades form a close phylogenetic unit; in this respect our basic philosophy more closely resembles that of Smith (1985) and Smith and Jell (1990) than that of Bell (1976a, 1980). We make the following observations as justification for taking this approach. Many widespread plesiomorphies are apparent in the character matrix developed for the cladistic analysis, indicating that the basic construction of the taxa studied is quite uniform (Fig. 1). Many traditional familial level taxa are "defined," at least in large part, not on shared derived characters but rather on unique character combinations; individual characters themselves are often plesiomorphic at some higher level; in fact, there are often few defining apomorphic characters (see Edrioasteroid Phylogeny). We have reduced most traditional families to subfamilial rank and reduced higher-level taxa accordingly. In addition to philosophical considerations, our classification differs from that of Bell (1980) in that the parsimony analysis mapped cyathocystids as derived from edrioas-

terids rather than isorophids, and edrioblastoids were specialized edrioasterids rather than a separate class. The classification offered by Smith is an abbreviated phylogenetic version. It differs most significantly from ours in combining pyrgocystids and cyathocystids as an order, in its inclusion of the cyclocystoids as a family within the isorophids, and in placing lebetodiscids as a subfamily within the Agelacrinitidae. A compilation of edrioasteroid genera included within families of the traditional classification is listed in the Appendix. (A few genera listed in the Appendix fall outside of the existing familial nomenclature listed below, but we have not erected a new classification scheme to receive them because this exceeded the focus of this paper.)

The Linnaean systematic classification adopted here is as follows:

- Class EDRIOASTEROIDEA Billings, 1858
 - Order CAMPTOSTROMATOIDA Durham, 1966
 - Family CAMPTOSTROMATIDAE Durham, 1968
 - Order STROMATOCYSTITIDA Bell, 1980
 - Family STROMATOCYSTITIDAE Bassler, 1935
 - Order ISOROPHIDA BELL, 1976
 - Family AGELACRINITIDAE Chapman, 1860 (emend.)
 - Family LEBETODISCIDAE Bell, 1976 (nomen transl., emend.)
 - Subfamily LEBETODISCINAE Bell, 1976 (nomen transl.)
 - Subfamily CARNEYELLINAE Bell, 1976 (nomen transl.)
 - Subfamily PYRGOCYSTINAE Kesling, 1967 (nomen transl., emend.)
 - Order EDRIOASTERIDA Bell, 1976 (emend.)
 - Suborder EDRIOASTERINA Bather, 1898 (nomen transl., emend.)
 - Family TOTIGLOBIDAE Bell and Sprinkle, 1978
 - Family EDRIOASTERIDAE Bather, 1898
 - Suborder EDRIOBLASTOIDINA Fay, 1962 (nomen transl., emend.)
 - Family ASTROCYSTITIDAE Bassler, 1935 (emend.)
 - Family CYATHOCYSTIDAE Bather, 1899 (emend.)
 - Subfamily CYATHOCYSTINAE Bather, 1899 (nomen transl., emend.)

Subfamily RHENOPYRGINAE Hollo-
way and Jell, 1983 (nomen transl.,
emend.)

Systematic Paleontology

Subphylum ECHINOZOA Matsumoto, 1929 Class EDRIOASTEROIDEA Billings, 1858 Order EDRIOASTERIDA Bell, 1976 (emend.)

DIAGNOSIS—Edrioasteroids with globular, bud-shaped, or turret-shaped theca; oral frame containing five compound interrarial elements, hydropore a fixed slit or pore through a single plate or shared by two plates immediately below the oral area in the posterior interarray, ambulacra with alternating plate biseries, cover plates without internal extensions, oral plating nondifferentiated except five interrarial orals extended to meet per-radially in some taxa, biserial floor plates separate or fused, with sutural passageways; poorly organized periproct, plate ring and collar derived from adhesion disc.

DISCUSSION—The Edrioasterida comprise a diverse assemblage of taxa, including edrioasterids, edrioblastoids, and cyathocystids. They range in age from Middle Cambrian through Late Ordovician.

Suborder EDRIOASTERINA Bather, 1898 (nomen transl., emend.)

DIAGNOSIS—Edrioasterids with globular or bud-shaped theca, oral frame with five compound interrarial plates and usually five compound radial plates, hydropore a slit shared across two plates; floor plates biserial with sutural pores, lower theca incurved toward adhesion disc with stout plate ring or, later, modified to distal plate ring and collar with interior attachment surface nonplated, collar can be elongated into stalk.

DISCUSSION—This taxon is essentially equivalent to Bather's family Edrioasteridae as defined by Bell (1976a, 1980) but is expanded to include their progenitors, the family Totiglobidae. The group ranges from Middle Cambrian to Middle Ordovician in age.

Family EDRIOASTERIDAE

Bather, 1898

DISCUSSION—See revised diagnosis in Bell (1976a, p. 291).

Genus *Paredriophus*

Guensburg and Sprinkle, new genus

TYPE SPECIES—*Paredriophus elongatus* Guensburg and Sprinkle, new species.

DIAGNOSIS—Theca elongate, bud-shaped; ambulacra long, apparently straight, raised, only one set of cover plates; interambulacra flat to slightly concave with fairly large tessellate plates, periproct low on CD interray; short attachment collar of tiny imbricate plates at base of theca; oral cover plates similar to those of *Edriophus*.

OCCURRENCE—Early Ordovician, western Utah, USA.

ETYMOLOGY—*Par-* meaning similar to the genus *Edriophus* from the Middle Ordovician.

DISCUSSION—*Paredriophus* is intermediate between Middle Ordovician edrioasterids, including *Edrioaster* and *Edriophus*, and the Middle Cambrian *Totiglobus*. It is closest to the former genera but differs from these in having a more elongate thecal shape with straight ambulacra and a short recurved lower theca (“resting zone” of Bell, 1976a). *Paredriophus* has a similar thecal shape and ambulacral distribution to *Totiglobus*, but the latter taxon has slightly imbricate interambulacral plating and small secondary cover plates and is attached by a small button-shaped adhesion disc rather than an attachment collar. It is not known if *Paredriophus* had a differentiated basal plate ring above the collar, but judging from related taxa we suspect that it did.

Paredriophus elongatus, new species

Figures 4–6

DIAGNOSIS—Edrioasterids with elongate theca having L/W value about 1.33; ambulacra apparently straight, extending nearly down sides of theca

for most of their length; thecal plates finely pitted; attachment collar fairly short with tiny imbricate plates, not hidden by theca above.

MATERIAL AND DESCRIPTION—Eight specimens available for study; five nearly complete thecae on one slab, most of these about same size, four upright and vertically distorted, one on its side (holotype) with part of collar exposed; whereas some thecal areas well preserved, exposed surfaces (downward-facing originally?) extensively corroded. Two small poorly preserved specimens, originally associated on small slab but now separate, are tentatively referred to this species. One isolated larger theca crushed with oral surface jumbled, aboral ambulacra and collar on opposite side better preserved.

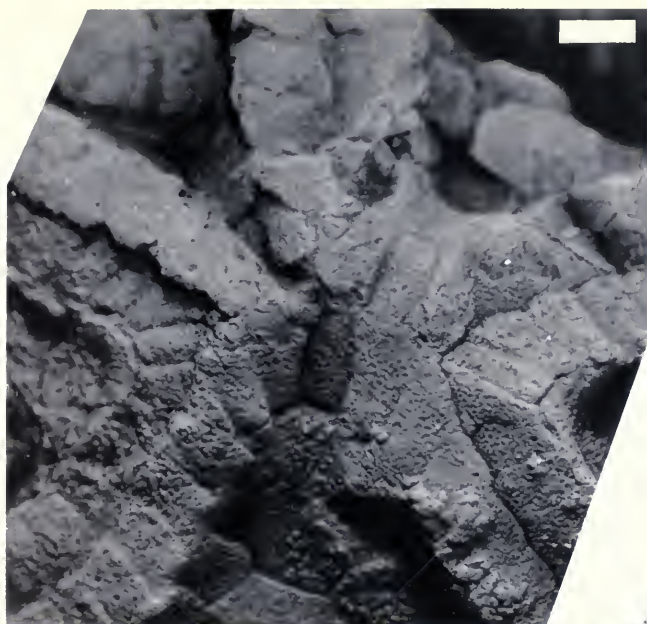
Theca bud-shaped, holotype thecal length about 20 mm without attachment collar, width about 15 mm (distorted by partial crushing), L/W value now about 1.33, original value perhaps 1.4–1.5, maximum diameter about $\frac{2}{3}$ way down theca; separate paratype PE 52683 approximately 50% larger, preserved width now 34 mm (badly crushed). Most thecal plates of moderate thickness (not as thick as those of *Edrioaster* and *Edriophus*) except for attachment collar, fine-pitted ornament preserved only in few areas.

Ambulacra long, wide, raised; straight in holotype and paratype PE 52686, curved slightly clockwise in crushed paratypes PE 52682–52685; constant width of about 4.0 mm in holotype for most of length, bluntly tapering near tips.

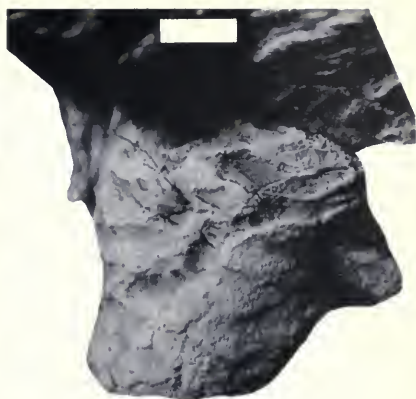
Oral area poorly preserved on most specimens except paratype PE 52682; oral plates nondifferentiated, similar to and continuous with cover plates, shape and arrangement essentially that of *Edriophus levis* (see Bell, 1976a, text Fig. 2a). Hydropore poorly exposed in paratype PE 52683, apparently an elongate slit shared and bisected by CD interradian frame plate and right posterior hydropore plate; secondary oral cover plate separated from oral area by lateral floor plate extension; second paratype PE 52682 apparently lacking secondary hydropore plate, instead hydropore slit shared by CD interradian frame plate and adjacent floor plate, well separated from oral area.

Cover plates arranged in simple alternating bi-

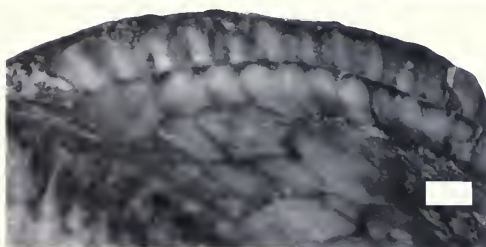
FIG. 4. *Paredriophus elongatus*, n. gen. and sp. A, Paratype PE 52682, oral area, compare to drawing in Figure 5. Scale bar = 1 mm. B, C, Holotype PE 52681, showing portion of plate collar (B) and ambulacrum and interambulacrum immersed in water (C). Scale bars = 1 mm. D, Paratype PE 52686, crushed lower surface, large specimen showing attachment surface of plate collar, straight ambulacra. Scale bar = 5 mm. E, Holotype PE 52681 (right center) and paratypes PE 52682–52685 cluster in near life position. Scale bar = 5 mm.



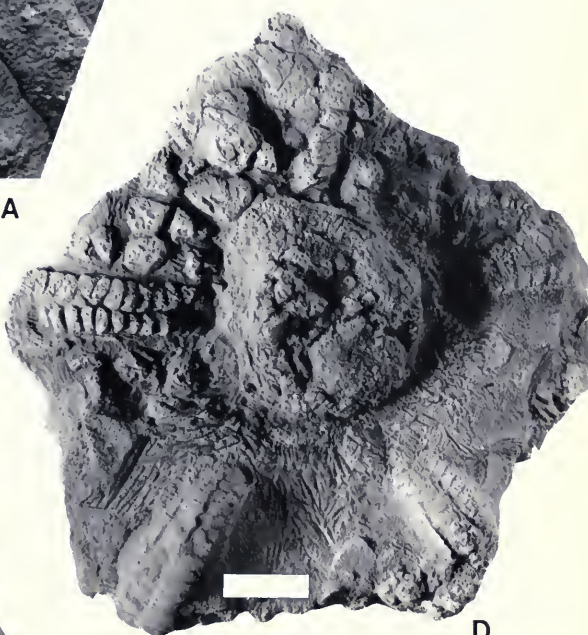
A



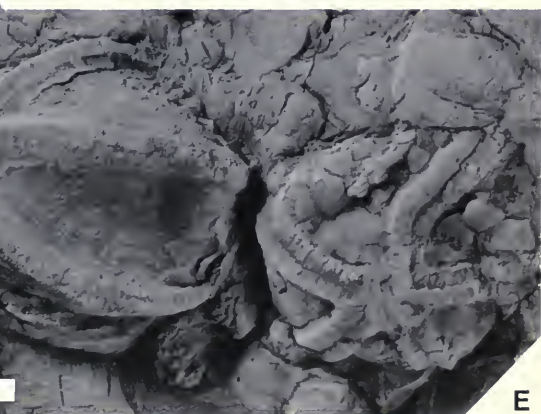
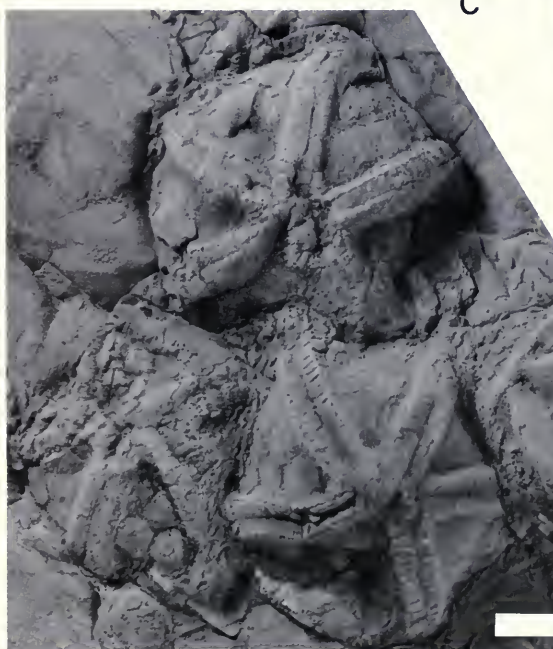
B



C



D



E

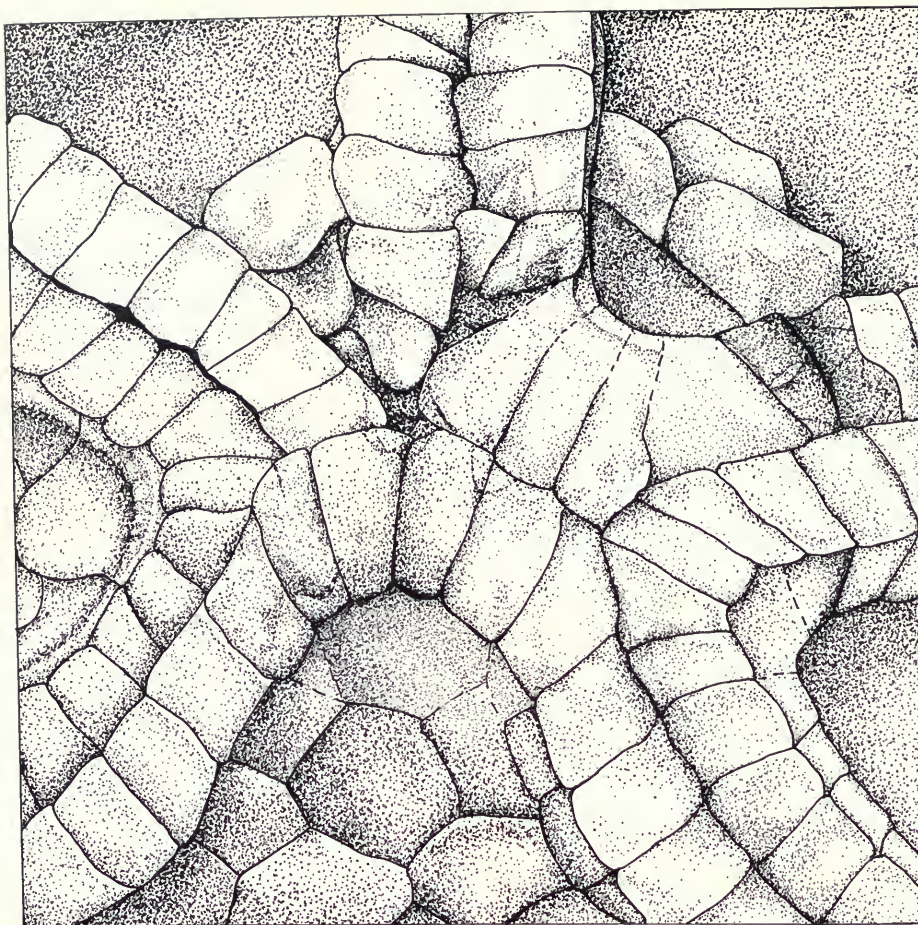


FIG. 5. *Paredriophus elongatus*, n. gen. and sp., oral area of paratype PE 52682 showing that basic plating arrangement is similar to that of the Middle Ordovician *Edrioaster* and *Edriophus*; shifting of plates has disrupted plating patterns around the A ambulacrum, cover plates have shifted over floor plate lateral extensions, and the hydropore is not preserved; dashed lines are inferred plate boundaries. Scale bar = 1 mm.

series, nearly flat, quadrangular, nearly twice as long as wide over most of ambulacral length, gently sinuous perradial suture, numerous small granular ossicles along well-preserved perradial suture and extending to oral area of holotype.

Only exterior abradial portions of floor plates exposed, concave, leading up to cover plates above in one-to-one arrangement, exposed portion varying in width, averaging about half width of adjacent cover plates.

Periproct poorly known, exposed only in paratype PE 52683, located about halfway down theca near center of posterior interray, preserved as radiating lath-shaped plates approximately 2 mm in diameter.

Interambulacral regions relatively narrow compared to *Edriophus*, flat to slightly concave in slightly distorted holotype, approximately 2.5 times longer than wide, containing approximately 45 tessellate plates on best side of holotype.

Lower theca below ambulacra not exposed in most specimens but no evidence of plate ring observed; holotype and largest paratype showing short collar of numerous, small, thin, squamose plates, diameter of collar approximately $\frac{2}{3}$ of thecal diameter above, in holotype, collar about 12 mm wide with an exposed length of about 6 mm, basal disc apparently fully plated in largest paratype.

OCCURRENCE—Five of the eight specimens assigned to this species, PE 52681–52685, are clus-

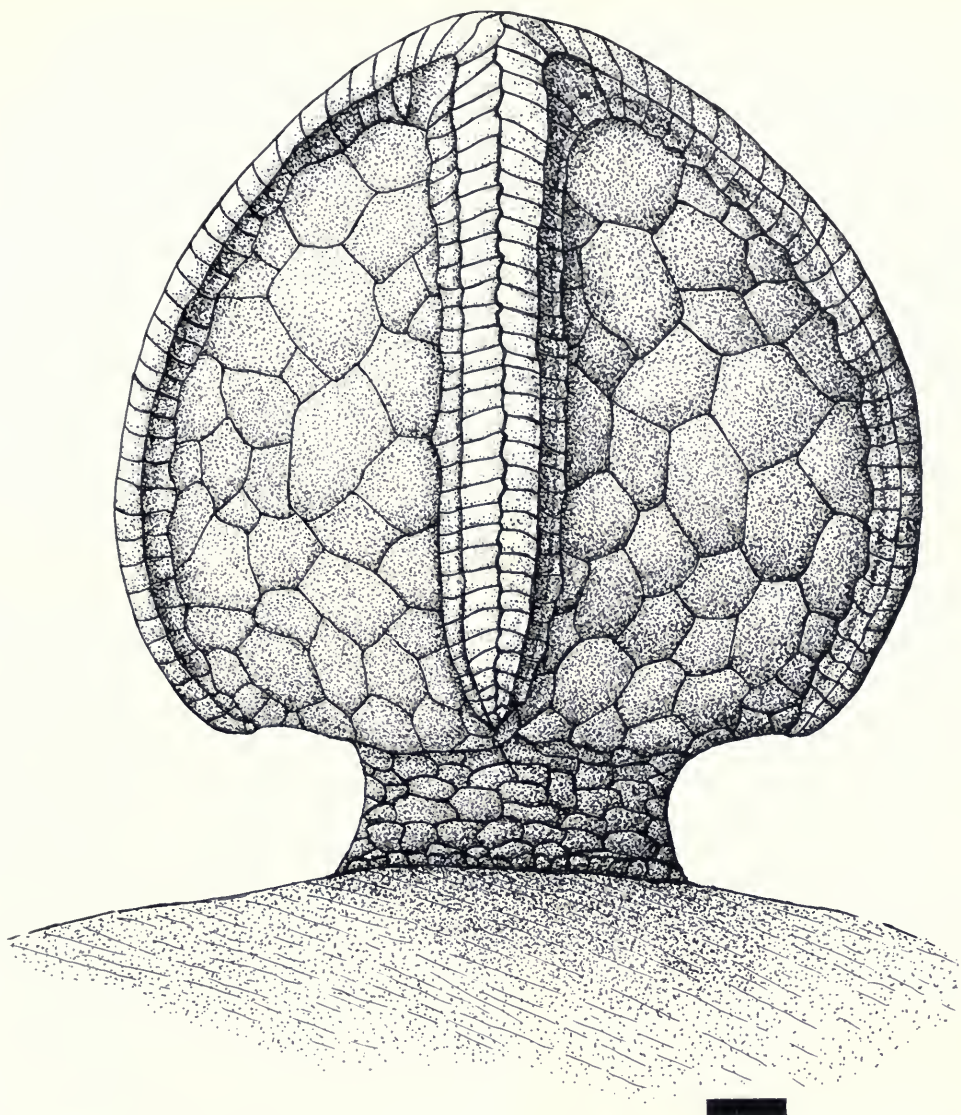


FIG. 6. Lateral reconstructed view of *Paredriophus elongatus*, n. gen. and sp., based primarily on holotype PE 52681 and paratype PE 52683, showing elongate bud-shaped theca and straight ambulacra, thecal shape is similar to *Totiglobus* from the Middle Cambrian; attachment collar length and shape are uncertain, but collar was likely short as shown. Scale bar = 1.5 mm.

tered together on a thin calcarenite bed found by Colin Sumrall. Shale covers the calcarenite surface, obscuring the exact nature of attachment, but four of the specimens remain erect and in their original position. The single large loose specimen was found separately and preserves the basal disc and collar. The two smaller specimens add little, if any, additional information. The stratigraphic horizon for these fossils is the uppermost trilobite

zone E, probably in the beds immediately overlying "Hintze's Reef" in the basal ledge-forming limestone member of the Fillmore Formation, Middle Ibexian (latest Tremadocian), Lower Ordovician (Hintze, 1973). Most specimens were found in fill dumped along the south side of U.S. Routes 6 and 50 just east of largest roadcut (collection locality 4 of Braithwaite, 1976) where "Hintze's Reef" is exposed at Skull Rock Pass;

two fragmentary specimens were found on a small slab from similar dumped fill along the north side of Routes 6 and 50 to the west of the roadcuts. The 6-50 east locality is in the SW SW, sec. 29 (unsurveyed), T20S, R13W, about 86 km (54 mi) southwest of Delta, Millard County, western Utah, USA.

SPECIMENS STUDIED—Holotype FMNH PE 52681, paratypes PE 52682–52689.

ETYMOLOGY—From the Latin *elongatus*, meaning prolonged or elongate, in reference to the thecal shape.

DISCUSSION—See Discussion under Genus *Par-edriophus*.

Edrioasterid Species Indeterminate

DISCUSSION—A number of partial edrioasterid specimens were recovered from three horizons in the middle Fillmore Formation. Disarticulated edrioasterid debris is also common throughout much of this part of the section but can be recognized only with close inspection (Fig. 7G). None of the partial specimens can be assigned to genus with confidence. Specimens from each of the three productive horizons differ in details, and multiple species appear to be represented. Despite the poor preservation, the specimens provide important information regarding edrioasterid morphology, ontogeny, and paleoecology. Each of the three occurrences are described and discussed separately below.

“Giza Peak” Megaripple Group Figures 7A, D

MATERIAL AND DESCRIPTION—This group is represented by three partial specimens, two of which provide significant information. One is a large flattened individual with much of the oral

surface preserved, but only parts of two ambulacra and one interambulacrum are well exposed; the second specimen is a well-preserved interior of the oral and adjacent areas. Theca large, flattened, partial specimen 43 mm wide, plates relatively thin (as compared to *Edrioaster* or *Edriophus*) with coarse pustulose ornament, ambulacra long, wide, nearly parallel-sided in midsection, curved counterclockwise in one example; oral frame a rigid raised ovoid funnel as viewed from interior, apparently composed of five radial and five inter-radial elements, posterior lip opening a low notch, stone canal passageway a small elliptical opening along the right posterior margin of the oral frame, ambulacral cover plates arranged in single alternating biseries, approximately 1.8 times wider than long over midsection of ambulacrum, tiny granular plates along perradial suture, floor plate extensions forming inclined surfaces abradial to cover plates, approximately $\frac{1}{3}$ width of adjacent cover plates, biserial floor plates forming inverted low V shape as viewed from below, sutural pores large, elliptical.

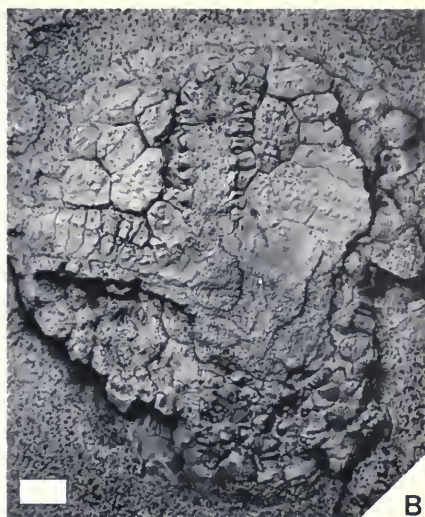
DISCUSSION—The large size of these fossils suggests they were adults. The counterclockwise ambulacral curvature and coarse pustulose ornament are suggestive of *Edrioaster*, but the relatively thin thecal plates and tiny granular plates along the perradial suture are more like those of *Paredriophus*. The stone canal passageway is proportionally smaller than that of *Edriophus* (see Bell, 1976a, Pl. 61).

OCCURRENCE—All three specimens were associated on the surface of a megaripple bed. None are attached, nor are any of the associated crinoids, suggesting transportation prior to burial. The collecting horizon is designated the “Giza Peak” megaripple bed and is in the lower part of the light gray ledge-forming member about 251 m above the base of the Fillmore Formation, trilobite zone G-2, Middle Ibexian (basal Arenigian), Lower Ordovician. The collecting locality is in the NW NE NW, sec. 25 (unsurveyed), T20S, R14W, northern Ibex area, House Range, Millard Co., western Utah, USA. This horizon has also produced the *Lam-*

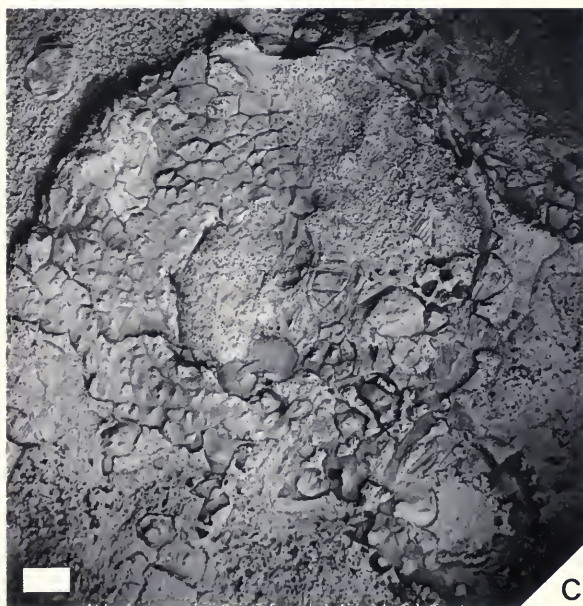
FIG. 7. Edrioasterid spp. indet. Scale bars = 2 mm. A, D, “Giza Peak” megaripple group. A, PE 52690, interior oral surface; D, PE 52691, partial specimen showing counterclockwise ambulacral curvature, adjacent interambulacra, and pustulose ornament. B, C, E, F, “Windy Point” hardground group. B, PE 52693, oral surface of poorly preserved large specimen. C, PE 52694, interior of lower theca. Note central opening for plate collar. E, PE 52695, extensively corroded juvenile showing rapidly tapering ambulacra and oral frame plates. F, PE 52696, relatively well-preserved juvenile showing large interradian oral frame plate, rapidly tapering ambulacra, and (?) pustulose ornament. G, PE 52717, isolated interradian oral frame plate, Pyramid Section of Datillo (1993).



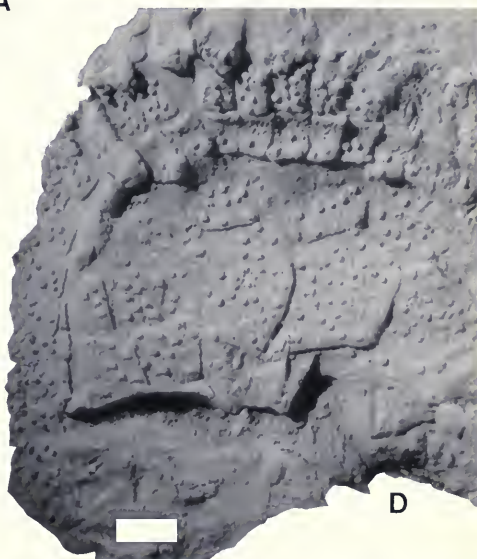
A



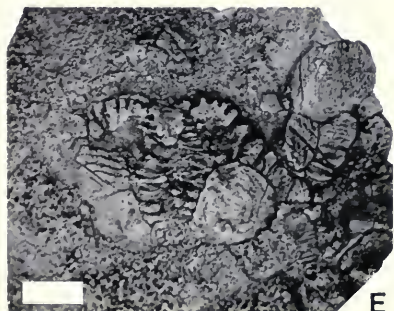
B



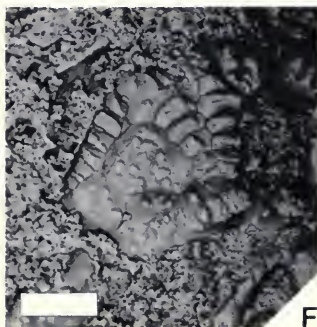
C



D



E



F



G

pteroblastus specimen at the “Windy Point North” locality nearby.

SPECIMENS STUDIED—The three specimens are FMNH PE 52690–52692.

“Windy Point” Hardground Group Figures 7B, C, E, F

MATERIAL AND DESCRIPTION—Hypodigm represented by 11 partial to nearly complete specimens; 4 are poorly preserved adults with upper parts of thecae mostly to completely stripped away, the remaining specimens are juveniles, most of which remain partly to nearly completely buried in indurated matrix; preservation of all specimens is typically poor because of calcite overgrowths and/or etching. Theca up to 19 mm in diameter in largest partial specimen, juveniles with minimum diameter of 5 mm; plates apparently thick, with pustulose ornament on interambulacra, partial ambulacra in one specimen straight or slightly curved, parallel-sided in midsection; floor plates biserial with sutural pores; recurved lower theca beyond ambulacra consists of numerous small, tightly sutured plates, sutures slightly inclined, basal ring with raised lip surrounding non-plated circular central opening; juveniles with nearly hemispherical upper surfaces, oral area large, oral frame with both radial and interradial elements, much larger than adjacent floor plates, oral cover plates apparently thin, arranged as in adult edrioasterids, ambulacra rapidly tapering, consisting of as few as six or seven floor plate pairs; interambulacra triangular, with few plates, proximal interambulacra very large, contacting inter-radial frame plate and several floor plates.

DISCUSSION—These edrioasterids provide the first information regarding edrioasterid ontogeny. The specimens remain attached to a hardground even though upper surfaces of larger individuals were removed prior to burial (see Brett & Liddell, 1978, for a similar occurrence). The ontogeny of juvenile edrioasterids followed a progression similar to that of isorophids (Bell, 1976b): few plates, a large oral area, and rapidly tapering ambulacra. The morphologic information available in these specimens is scant and could be referable to any Early or Middle Ordovician edrioasterid genus.

OCCURRENCE—All specimens were found by Guensburg in close association over a total area of less than 0.5 m² on a hardground designated

the “Windy Point” hardground. A few crinoid fragments also occur in association with the edrioasteroids. The horizon and age are as follows: just above the base of the brown slope and ledge member (Hintze, 1973), about 314 m above the base of the Fillmore Formation, in trilobite zone G-2, Middle Ibexian (lower Arenigian), Lower Or-Ordovician. The “Windy Point” hardground locality is on a steep ridge in the SW SE NE, sec. 25 (unsurveyed), T20S, R14W, northern Ibex area, House Range, Millard Co., western Utah, USA.

SPECIMENS STUDIED—The specimens are catalogued as FMNH PE 52693–52703.

“Giza Peak” Mound Specimen

MATERIAL AND DISCUSSION—This single partial specimen preserves articulated interambulacral plates and adjacent parts of one ambulacrum. It differs from other edrioasterids from the middle part of the Fillmore in having smooth plates. It is preserved on a localized, high-relief, *Calathium*-stromatolitic mound (see Church, 1974).

OCCURRENCE—The single specimen is from “Church’s Reef”; discontinuous mounds extend across most of the Ibex area at this horizon. Several partial iocrinid fragments were found in association with this specimen. “Church’s Reef” is in the upper part of the slope-forming shaly siltstone member (Hintze, 1973) about 240 m above the base of the Fillmore Formation, trilobite zone G-2, Middle Ibexian (lowest Arenigian), Lower Ordovician. The “Giza Peak” locality is in the NW NE NW, sec. 25 (unsurveyed), T20S, R14W, northern Ibex area, House Range, Millard Co., western Utah, USA.

SPECIMEN STUDIED—The single specimen is catalogued as FMNH PE 52704.

Suborder EDRIOBLASTOIDINA Fay, 1962 (nomen transl., emend.)

DIAGNOSIS—Edrioasterid edrioasteroids with bud-shaped to turret-shaped theca, interradial oral frame plates usually fused to floor plates forming deltoids, five interradial oral cover plates expanded meeting centrally over the mouth, hydropore

not identified with certainty, possibly pore through deltoid, sutural pores between floor plates shifted abradially.

DISCUSSION—This suborder is emended to receive both traditional edrioblastoids and cyathocystids. It ranges in age from Late Cambrian to Early Devonian.

Family CYATHOCYSTIDAE **Bather, 1899 (emend.)**

DIAGNOSIS—Edrioblastoids with turret-shaped theca and nearly flat to slightly domal oral surface, oral plating reduced with deltoids occupying entire interambulacra, oral cover plates cover much of oral surface, ambulacra rapidly tapering, collar expanded to form cylindrical sides and bottom of theca, basal ring surrounds margin of oral surface of certain species.

DISCUSSION—Cyathocystids are remarkably widespread, particularly given their low diversity of only *Cyathocystis* and *Rhenopyrgus*. These two genera differ considerably in construction of the elongate thecal structures and consequently we have assigned them to separate subfamilies. *Cyathocystis* is characterized by fusion of the entire side and bottom portion of the theca into a solid cup, whereas in *Rhenopyrgus* the sides of the theca consist of imbricate plates and the base of the theca is expanded to form a coriaceous sac. *Cyathotheca* Jaekel, 1927, is closely related to or more likely a junior synonym of *Cyathocystis*, differing from the latter only in lacking a basal ring. This apparent difference could be purely preservational (Fig. 17D). This group ranges in age from Middle Ordovician to Early Devonian.

Subfamily CYATHOCYSTINAE **Bather, 1899** **(nomen transl., emend.)**

DIAGNOSIS—Cyathocystids with fused sides and bottom of the turret-shaped theca.

DISCUSSION—Cyathocystinids as defined here are equivalent to the family Cyathocystidae of Bather, 1898, and the order Cyathocystida, Bell, 1975 (see Bockelie & Paul, 1983). The group ranges in age from Middle to Late Ordovician.

Subfamily RHENOPYRGINAE **Holloway and Jell, 1983** **(nomen transl., emend.)**

DIAGNOSIS—Cyathocystids with imbricate sides of theca and a distal coriaceous sac.

DISCUSSION—Rhenopyrginids are as yet represented only by *Rhenopyrgus* itself. This subfamily has been discussed at length by Holloway and Jell (1983, pp. 1002–1004) as their family Rhenopyrgidae. The group ranges from the Late Ordovician to Early Devonian in age.

Family ASTROCYSTITIDAE **Bassler, 1935 (emend.)**

DIAGNOSIS—Edrioblastoids with a bud-shaped theca, ambulacra raised above level of surrounding theca, interambulacral plates arranged in circlets with five basals below, theca elevated by a stalk with plate mosaic or columnals.

DISCUSSION—Only three genera of edrioblastoids are known: *Astrocystites*, *Cambraster*, and *Lampteroblastus*. Rosznov (written comm., January 1993) has reported two other genera from the Early Ordovician, but to our knowledge these are not described. “*Totiglobus*” *lloydi* from the Middle Cambrian of Utah could be a primitive edrioblastoid, but we prefer not to assign it at this time because of poor preservation and nonspecialized construction. Aside from this genus, edrioblastoids range in age from Late Cambrian to Late Ordovician.

Genus *Lampteroblastus* **Guensburg and Sprinkle, new genus**

TYPE SPECIES—*Lampteroblastus hintzei* Guensburg and Sprinkle, new species.

DIAGNOSIS—Astrocystitid edrioblastoid with elongate, cylindrical theca; ambulacra straight, short, rapidly tapering, tips curled a short distance down from summit; cover plates biserial, oral cover plates nondifferentiated; interambulacra occupied by single triangular deltoid; six alternating plate circlets in mid-to-distal theca; no respiratory pores visible; stalk well defined, narrow, tapering, composed of cuneate plates forming a chevron pattern.

OCCURRENCE—Early Ordovician, western Utah, USA.

ETYMOLOGY—From the Greek *lampteros*, torch, lamp, and the Greek *blastos*, bud, for the elongate bud-shaped theca.

DISCUSSION—*Lampteroblastus* can easily be distinguished from other edrioblastoids. The Middle Ordovician *Astrocystites* has a more rounded bud shape with ambulacra extending well down the sides of the theca, expanded interrational oral cover plates, parabolic deltoids, multiplated interambulacra, fewer theca plates with only two plate circlets below the ambulacra, and respiratory pores at triple junctures of interambulacral plates. The apomorphies of *Lampteroblastus* such as highly elongate theca, triangular deltoids, and short ambulacra differ greatly from *Astrocystites*, and we conclude these two genera are not closely related within the astrocystitids. The Late Cambrian *Cambroblastus* is far more primitive than *Lampteroblastus* and can be identified by its longer ambulacra extending well down the thecal sides, biserial nonfused ambulacral floor plates, multiplated interambulacra, three plate circlets below the ambulacra, and irregularly plated stalk. *Cambroblastus* is a plausible progenitor of both *Astrocystites* and *Lampteroblastus*. The nonspecialized cover plate arrangement of *Lampteroblastus* is most like that of *Cambroblastus*. Beyond the edrioblastoids proper, cyathocystids also have large triangular deltoids generally similar to those of *Lampteroblastus*.

Lampteroblastus hintzei, new species

Figures 8A–D, 9

DIAGNOSIS—Same as that of genus.

MATERIAL AND DESCRIPTION—The only specimen available for study is the complete and well-preserved holotype; it is preserved on its side on a small slab with the CD interray, two ambulacra and part of the oral surface buried in hard matrix.

Holotype theca 16 mm in length and maximum 9 mm wide 3 mm below summit; theca nearly cylindrical, pentagonal in oral view, oral region large, nearly as wide as each ambulacrum, distal theca conical, stem facet small; all plates tessellate, lower thecal plates heavily ridged.

Ambulacra five, short, 7 mm long, straight, raised above deltoids, arranged in 2–1–2 pattern, rapidly tapering away from oral area, confined to near thecal summit; oral cover plates not differentiated, five interrational orals apparently meet centrally over mouth, approximately 20 cover plates per ambulacrum, arranged in single alternating biseries, meeting at sinuous perradial suture, approximately 4 times wider than long proximally, becoming longer than wide at ambulacral tips; ambulacral groove exposed along broken ambulacrum tip only, apparently deep, V-shaped.

Large triangular deltoids fill interambulacral areas, 3.0 mm long and 4.3 mm wide in two exposed areas, nearly flat except for medial indentation; medial and lower theca of six alternating plate circlets in radial and interrational positions, apparently five plates per circlet; three circlets in radial position stacked, proximal radial circlet small trapezoidal plates immediately below ambulacra in open circlet, followed distally by larger octagonal to heptagonal plates in complete to slightly open circlet, and then larger heptagonal plates in open circlet; three interrational plate circlets separated (orally-aborally), adoral circlet open, of inverted triangular or pentagonal plates, next aboral circlet open, of slightly larger quadrangular plates with prominent X-ridges, aboralmost circlet of large, tall, pentagonal plates (basals), forming conical thecal base; hydropore and periproct not exposed.

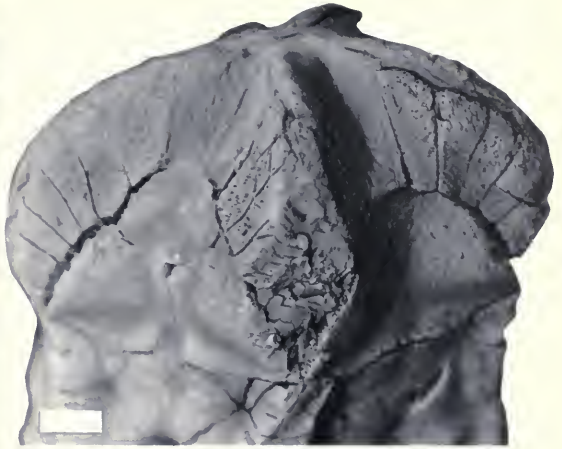
Only short proximal stem segment preserved, of small smooth wedge-shaped plates arranged in crude chevrons.

OCCURRENCE—The single specimen found by Guensburg is from the top of the “Giza Peak” megaripple bed at the “Windy Point North” locality of our field notes. This bed occurs locally 251 m above the base of the Fillmore in the lower

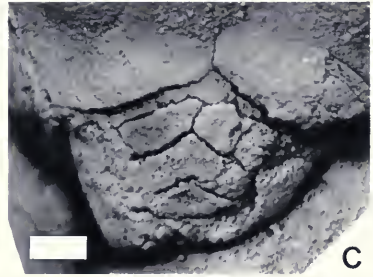
FIG. 8. A–D, *Lampteroblastus hintzei*, n. gen. and sp., holotype PE 52705. A, Complete specimen in lateral view, compare to drawing in Figure 9A. Scale bar = 1 mm. B, Oblique view of summit; compare to drawing in Figure 6B. Scale bar = 1 mm. C, Proximal stem segment with chevron-shaped plates. Scale bar = 0.5 mm. D, Complete specimen immersed in water. Note triangular deltoids. Scale bar = 2 mm. E, F, *Deltadiscus superbus*, n. gen. and sp., holotype PE 52706. E, Entire specimen, periproct just below oral area (see Fig. 10A for details). Scale bar = 2 mm. F, Detail of ambulacrum (see Fig. 10B for details). Scale bar = 1 mm.



A



B



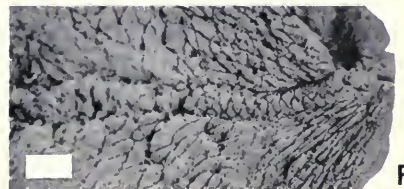
C



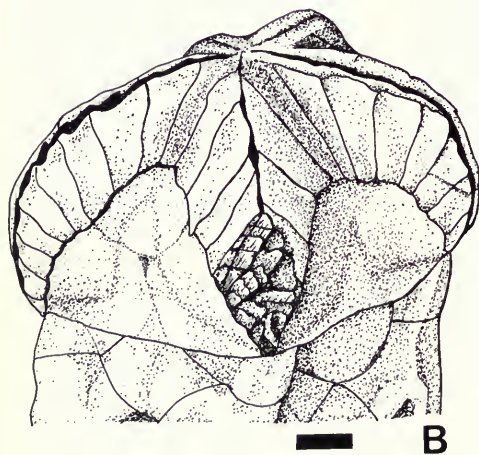
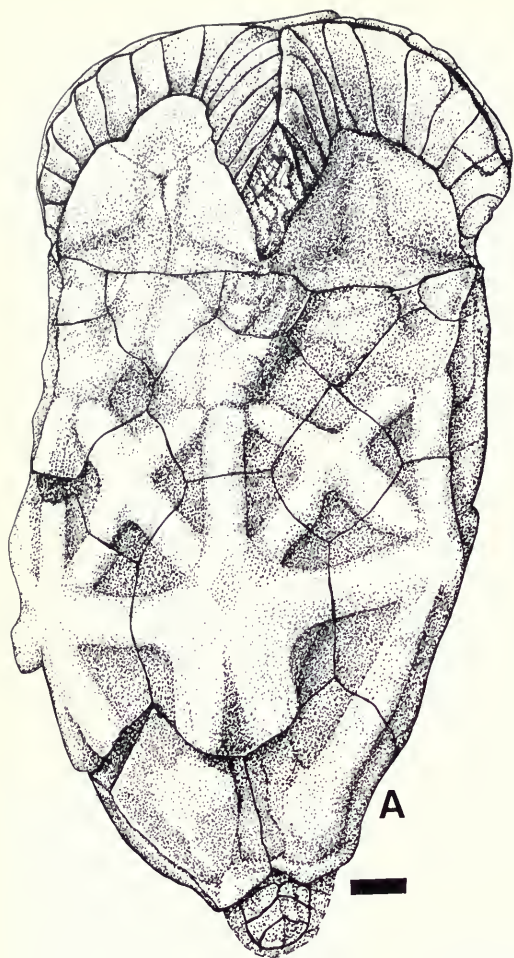
D



E



F



part of the light gray ledge-forming member of the Fillmore Formation, trilobite zone G-2, Middle Ibexian (basal Arenigian), Lower Ordovician (see Hintze, 1973). This locality is in the SE NW NE, sec. 25 (unsurveyed), T20S, R14W, Millard Co., western Utah, USA.

SPECIMEN STUDIED—The holotype is catalogued as FMNH PE 52705.

ETYMOLOGY—Named for Lehi F. Hintze, who studied and recognized the importance of Early Ordovician rocks and their faunas in western Utah. The stratigraphic framework erected by Dr. Hintze was of invaluable help in this research.

DISCUSSION—See Discussion under Genus *Lampteroblastus*.

Order ISOROPHIDA

Bell, 1976

Family AGELACRINITIDAE

Chapman, 1860 (emend.)

DIAGNOSIS—Isorophida with domal or clavate theca, several (minimum of four) differentiated oral cover plates, hydropore bordered by few to several plates, ambulacra nearly always thin, slightly raised above or even with adjacent interambulacra, ambulacral cover plates rarely forming simple alternating biseries, or nearly always a double alternating biseries or more complex cyclic biseries, cover plates with internal extensions, no intrathecal cover plate passageways, ambulacral floor plates usually abutting along vertical suture, periproct valvular or semivalvular.

DISCUSSION—The family Agelacrinitidae (Chapman, 1860) is the oldest family group name proposed for the included genera and was defined originally on all known edrioasteroids. Later authors have conserved the name but restricted the scope of this taxon to *Agelacrinites* and its close relatives. As conceived here, the Agelacrinitidae

FIG. 9. *Lampteroblastus hintzei*, n. gen. and sp., holotype PE 52705, plate cracks indicated by stippling. Scale bar = 1 mm. A, Lateral view, triangular deltoids filling interambulacra, lower theca dominated by plate circlets with trusswork of prominent ridges superficially resembling the pattern found on certain camerate crinoids such as *Lampterocrinus*, proximal stem with wedge-shaped plates. B, Oblique view of thecal summit and oral area. Note primary orals meeting centrally over mouth and simple cover plating.

is essentially equivalent to the suborder Isorophina Bell, 1976, or the subfamily Isorophinae Bell, 1976, of Smith (1985). We prefer this nomenclature because it conserves existing terminology and most reflects the close relationship of all included species (see Edrioasteroid Phylogeny). The agelacrinitids are by far the most successful of edrioasteroid clades and range in age from the Early Ordovician to Late Pennsylvanian.

Genus *Deltadiscus* Guensburg and Sprinkle, new genus

TYPE SPECIES—*Deltadiscus superbus* Guensburg and Sprinkle, new species.

DIAGNOSIS—Agelacrinitid edrioasteroid with flat-topped domal theca, small oral area with close 2–1–2 pattern, thin, straight ambulacra, cover plates irregular-shaped but arranged in simple alternating biseries; periproct with elongate plates in semivalvular arrangement; interambulacra broad, with numerous thin squamose plates, highly imbricate zone extending short distance beyond ambulacral tips, covering attachment structure.

OCCURRENCE—Early Ordovician, western Utah, USA.

ETYMOLOGY—Named for the town of Delta, Utah, our base of operations for our field work in the Ibex area.

DISCUSSION—The new genus is provisionally assigned to and arguably the most primitive taxon of agelacrinitids. Difficulties in evaluating this taxon result from the lack of or poor information regarding oral cover plate, hydropore, and peripheral rim construction and the fact that it retains primitive features lost by more advanced agelacrinitids such as nonuniform cover plates and semivalvular periproct. Alternatively, the thin ambulacra with no indication of intrathecal cover plate passageways suggest agelacrinitid affinities. The imbricate interambulacrals and thecal elongation zone beyond the ambulacra are derived and contrast sharply with the ambulacral construction. Consequently, we are unsure as to what later taxa, if any, *Deltadiscus* could have been ancestral to. The general size and distribution of the ambulacra of *Deltadiscus* are similar to primitive edrioasteroids such as *Stromatocystites* or *Edriodiscus*, but these taxa differ in many details, including low domal shape, irregular cover plates, and tessellate interambulacra. The Late Cambrian isorophids *Chatsworthia* and *Hadrodiscus* differ sub-

stantially in having erect ambulacra with thick biserial cover plates like those of lebetodiscids. Among advanced agelacrinitids, *Cooperidiscus* from the Devonian has extremely narrow ambulacra like *Deltadiscus*, but this taxon is also poorly known and has curved ambulacra, and even the cover plate arrangement cannot be discerned, so comparison is very limited. Typical agelacrinitids such as *Isorophusella* from the Middle Ordovician differ from *Deltadiscus* in having a low domal shape, much wider ambulacra and larger oral area, uniform cover plates arranged in a double biseries, and a valvular periproct.

Deltadiscus superbus, new species Figures 8E, F, 10

DIAGNOSIS—Same as that of genus.

MATERIAL AND DESCRIPTION—Only holotype known; thecal diameter 18 mm, slightly etched and flattened but complete and remarkably well preserved; theca subpentagonal in outline, domal with raised sides and slightly convex top in life; ambulacra long, thin, 1 mm wide just beyond oral area, straight, slowly tapering, slightly arched (pushed down distally to below level of interamb by flattening), oral area small so that 2–1–2 pattern of ambulacral juncture only vaguely defined, oral plating obscure, number and distribution of plates uncertain, hydropore oral probably small, oral frame not exposed; ambulacral cover plates form single alternating but nonuniform biseries, sharply oscillating perradial suture extends nearly full width of ambulacra, floor plates and features of ambulacral groove interior unexposed, assumed to be solid without cover plate passageways; periproct small, centrally situated in posterior interambulacrum, 1.8 mm in diameter, composed of approximately 15 irregular lath-shaped plates with elongate axes radiating from center; interambulacral areas large, formed by numerous small, thin imbricate plates (overlapping in oral direction), approximately 30 plates across interambulacrum at tips of ambulacra, similar plates continuing distally well beyond tips of ambulacra and curling over the thecal edge as preserved, forming short extendable pedunculate zone in life; attachment structure unexposed but presumably included a peripheral rim.

OCCURRENCE—The single specimen collected by Sprinkle is from 9 m above the base of the cal-

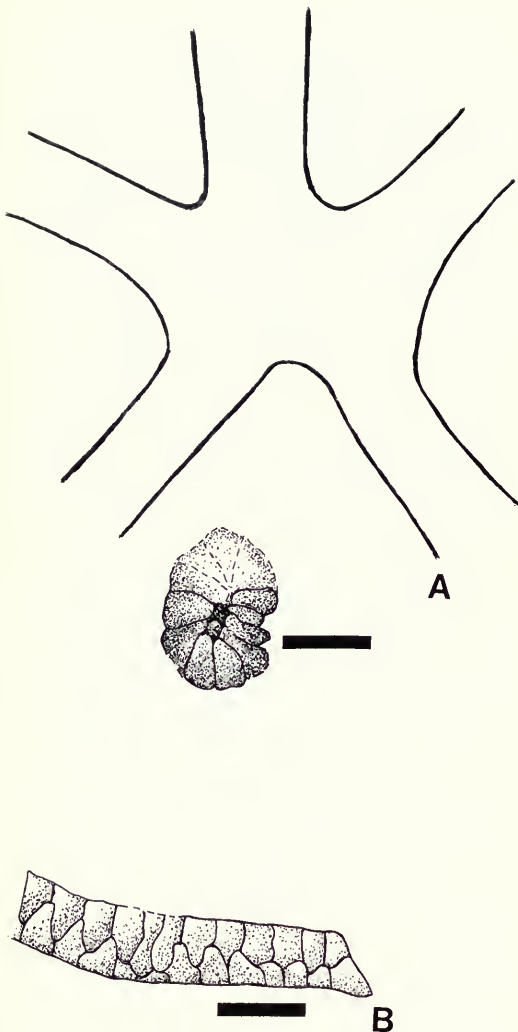


FIG. 10. *Deltadiscus superbis*, n. gen. and sp., holotype PE 52706. Scale bar = 1 mm. A, Periproct with numerous irregular lath-shaped plates and surrounding interambulacra. B, Cover plate arrangement of distal B ambulacrum showing poorly organized alternating biseries, perradial suture with strong zigzag pattern.

carenite member, trilobite zone H, Fillmore Formation, Upper Ibexian (Lower Arenigian), Lower Ordovician. It occurs on a moderately well-sorted calcarenite (grainstone) that appears to be largely composed of echinoderm debris. Well-sorted cross-bedded grainstones dominate this part of the Fillmore section. No other well-preserved macrofossils were associated with this specimen. The locality is on the measured section designated as

Square Top (Hintze, 1973) along the west flank of the southern House Range, in the NW SE SE, sec. 31, T21S, R13W, approximately 80 km southwest of Delta, Millard Co., western Utah, USA.

SPECIMEN STUDIED—The holotype is FMNH PE 52706.

ETYMOLOGY—*Superbus* refers to the outstanding preservation of the only known specimen, particularly given the highly agitated conditions that characterized paleoenvironments through the associated interval of the Fillmore Foundation.

DISCUSSION—See Discussion under Genus *Deltadiscus*.*

Family LEBETODISCIDAE Bell, 1976 (nomen. transl., emend.)

DIAGNOSIS—Isorophid edrioasteroids with domal to turret-shaped theca, three primary oral cover plates, hydropore structure typically bounded by few plates, thick ambulacral cover plates arranged in a single alternating biseries with intrathecal and intertheatal extensions, sutural passageways between cover plates, ambulacral floor plates imbricate or lost, periproct with poorly organized plating.

DISCUSSION—The family Lebetodiscidae as defined here is essentially equivalent to the suborder Lebetodiscina Bell, 1976, and defined in Bell (1980), where pyrgocystids were incorporated. The definition is modified slightly to include new findings regarding pyrgocystid morphology. Lebetodiscids range from the Late Cambrian to the Late Devonian.

* A second specimen referable to this taxon was discovered by Colin Sumrall while this paper was in press. It is 30 mm in diameter, and portions of four interambulacra, the distal tips of two ambulacra, and much of the peripheral rim are preserved intact. The thecal margin is ragged though well preserved, suggesting this configuration in life. The peripheral rim consists of six or seven imbricate plate rows. Peripheral rim plates merge with and are difficult to distinguish from adjacent interambulacra. The proximal circlet is not significantly thickened, unlike most isorophids. It occurred higher in the section than the holotype, on a hardground 3 cm above the *Calathium* reef, *Calathium* calcisiltite member, trilobite zone I, Fillmore Formation. The locality is in the NW, sec. 29, T21S, R13W, Millard Co., Utah. The specimen is designated as paratype FMNH PE 52719.

Subfamily LEBETODISCINAE

Bell, 1976

(nomen transl., emend.)

DIAGNOSIS—Lebetodiscids with domal theca, projecting and usually rounded ambulacra, usually two pairs of lateral shared cover plates and secondary orals, hydropore structure opening along adradial suture line of proximal part of ambulacrum V, composed of both interambulacral and ambulacral plates, cover plates thick, floor plates present, periproct flush or slightly raised, narrow peripheral rim, sometimes spinose oral surface.

DISCUSSION—The subfamily Lebetodiscinae is equivalent to the Lebetodiscidae Bell, 1976, but it is emended to allow for separation of pyrgocystinids (see below).

Subfamily CARNEYELLINAE

Bell, 1976

(nomen transl.)

DIAGNOSIS—Lebetodiscids with domal theca, slightly raised ambulacra, oral area lacking secondary oral plates or shared cover plates, plates covering ambulacral and hydropore areas moderate thickness, hydropore in right posterior oral region, large hydropore oral, periproct even with thecal surface.

DISCUSSION—This subfamily is equivalent to the family Carneyellidae Bell, 1976, and is again modified to distinguish the pyrgocystinids.

Subfamily PYRGOCYSTINAE

Kesling, 1967

(nomen transl., emend.)

DIAGNOSIS—Lebetodiscids with domal to turret-shaped theca; elongated pedunculate zone in some taxa, reduced oral area and short petaloid ambulacra, hydropore structure along adradial suture line of ambulacrum V, with single thick massive hydropore oral, ambulacral cover plates erect, thick, taller than wide with summits flattened, club-shaped, lateral hood plates, ambulacral floor plates lacking, periproct conical, and oral surface often spinose.

DISCUSSION—General similarity between pyrgocystinids and the lebetodiscinid *Cystaster* was

first noted by Kesling (1967, p. 201); later both Bell (1980, p. 160) and Holloway and Jell (1983, p. 1012) independently made similar observations linking pyrgocystinids with lebetodiscids. We agree; the parsimony analysis mapped pyrgocystinids branching from a lebetodiscid ancestor (Figs. 1, 2). They were in many ways the most specialized of lebetodiscids. Unique characteristics of the subfamily include the shape of the cover plates, lack of floor plates, and the addition of lateral hood plates; however, not all pyrgocystinids are turret-shaped, and this readily recognized characteristic is not diagnostic. Pyrgocystinids share similarities with lebetodiscinids such as *Cystaster* or *Streptaster*, including the elevated ambulacra with greatly thickened spine-bearing cover plates, tall narrow ambulacral tunnel, and diminutive oral area. The ambulacral floor plates of *Streptaster* are greatly reduced, and this trend is carried to its extreme in pyrgocystids, where they are lost entirely (see Bell, 1976, pl. 9). *Belochthos*, another lebetodiscinid, has short petaloid ambulacra generally similar to those of pyrgocystinids. *Chatsworthia*, from the Late Cambrian, branched as the sister group to lebetodiscinids in many trees in the parsimony analysis. It has greatly thickened cover plates arranged in an alternating biseries reminiscent of pyrgocystinids. Smith and Jell (1990, p. 741) noted the similarity of the cover plate plating of the lebetodiscinid *Foerstediscus* to that of *Chatsworthia*.

The extraordinarily revealing specimens of *Archaeopyrgus* and to a lesser extent *Fanulodiscus* provide the first opportunity to interpret pyrgocystinid functional morphology based on nearly complete and well-exposed oral morphology. Previous descriptions of *Pyrgocystis* species published over the past 80 years were based on poorly preserved material that resulted in sketchy definition of pyrgocystid characteristics and entanglement with the superficially similar but only distantly related *Rhenopyrgus* (see Regnéll, 1966; Holloway & Jell, 1983; Smith, 1985). *Rhenopyrgus* morphology has recently been used as the basis for defining pyrgocystinid morphology and relationships (Smith, 1985, p. 731). Holloway and Jell (1983) recognized the disparate nature of pyrgocystids and rhenopyrgids and placed them in separate families. The parsimony analysis supports this finding and placed these two groups in isorophid and edrioasterid clades, respectively (Figs. 1, 2). *Pyrgocystis* specimens often consist of the pedunculate zone only, and those preserving the

oral surface often have a dense covering of protective spines or are moldic; consequently, this taxon remains poorly known (see Fig. 12C). *Archaepyrigus* specimens not only provide a detailed external morphology but also many details of the thecal interior.

The oral surface of pyrgocystinids is unique among edrioasteroids. It is dominated by short petalloid ambulacra (Figs. 11A, B, 12C) in a compact configuration. This trend is fully developed in *Pyrgocystis*, where the exterior oral area is depressed and tiny so that each ambulacrum is essentially a separate disjunct structure in some ways reminiscent of the condition found in certain advanced fissiculate blastoids (Fig. 12C). The ambulacra in pyrgocystinids are constructed of tall, slab-like, biserial cover plates with planar cover plate crests that project well above the surrounding interambulacral areas. Internal cover plate passageways form gaps between successive cover plates, extend upward to near the cover plate surfaces, and presumably housed ciliated tissues enhancing feeding capacity and/or respiration (Bell, 1976a) (Fig. 12D). Cover plate extensions are expanded below (internally) both abradially and adradially. They meet perradially along a short suture, completely encircling the food groove. Presumably, rotation of cover plates through only a few degrees of arc facilitated feeding. Hood plates articulate with and support cover plates (Fig. 13); they are expanded at either end, and the resulting gaps could have enhanced respiration. In *Fanulodiscus* and *Pyrgocystis*(?) *petalus*, hood plates are preserved in their original position and form a channelway surrounding the ambulacra (Holloway & Jell, 1983, Fig. 5, Fig. 18). Striations are found on the hydropore oral plate of *Archaepyrigus* and *Pyrgocystis* specimens (Figs. 17C, E). They are apparently a diagenetic artifact but, if not, indicate this plate was porous. Lebetodiscids, including most pyrgocystinids, possessed articulating spines. Spines are largely concentrated atop cover plate crests in *Archaepyrigus*, some *Pyrgocystis* species, and *Epipaston*. They attached to interambulacral/pedunculate zone and peripheral rim plates in certain taxa (see Holloway & Jell, 1983, Fig. 3; Guensburg, 1988, Fig. 8.3). Their function seems to have been primarily protective, but Holloway and Jell (1983) suggested they could also conceivably have enhanced or directed feeding currents. Pyrgocystinids attached by a peripheral rim to hard surfaces, including skeletal fragments such as nautiloid conchs (*Archaepyrigus*, *Epipaston*), trilobite exuvae (*Archaepyrigus*, *Pyrgocystis*), brachiopod

valves (*Epipaston*), or hardgrounds (*Fanulodiscus*, *Archaepyrigus*).

Of the four genera included as pyrgocystinids, *Pyrgocystis* Bather and *Archaepyrigus*, n. gen., are cylindrical turret-shaped forms with a highly extensible pedunculate zone. These forms were capable of contracting to a considerable degree (Figs. 11D, 18). *Fanulodiscus*, n. gen., and *Epipaston* Holloway and Jell were domal forms capable of moderate shape change. As in other edrioasteroid clades, elongation potential among pyrgocystinids developed independently in a portion of the member taxa.

Genus *Archaepyrigus* Guensburg and Sprinkle, new genus

TYPE SPECIES—*Archaepyrigus anitae* Guensburg and Sprinkle, new species.

DIAGNOSIS—Pyrgocystinid edrioasteroids with ambulacra relatively narrow and oral area large, anal pyramid a protruding cone of lath-shaped plates, and (?) sparse spine covering on oral surface; theca low, turret-shaped when contracted.

OCCURRENCE—Early Ordovician, western Utah, USA.

ETYMOLOGY—*Archae* from Latin meaning old or ancient and *pyrgos* from Greek meaning tower.

DISCUSSION—The genus most closely resembling *Archaepyrigus* is *Pyrgocystis*, whose morphology, as previously stated, is poorly known. *Pyrgocystis* has distinctly more petalloid ambulacra and a diminutive oral area (see Figs. 11, 12C; Holloway & Jell, 1990, Fig. 5, for comparison), a smaller periproct, and more dense spination in some cases than *Archaepyrigus*. The oral area in *Pyrgocystis* has virtually been lost, so that the ambulacra are in effect disjunct. The relatively narrow ambulacra and large oral area of *Archaepyrigus* are plesiomorphic. Among other pyrgocystids, *Fanulodiscus*, n. gen., and *Epipaston* Holloway and Jell can easily be distinguished from *Archaepyrigus* by their domal rather than turret shape and proportionately large peripheral rims.

Archaepyrigus anitae, new species Figures 11, 12A,B, 13–16

DIAGNOSIS—Same as that of genus.

MATERIAL AND DESCRIPTION—Description based on 10 specimens in varying stages of preservation, several remain attached; theca small, low, turret-shaped, ranging from 8 to 14 mm and averaging 11.2 mm in width among five measurable specimens; partly collapsed holotype is 7 mm high and 8 mm wide, slightly contracted but undistorted; paratype is 3 mm high, oral surface outline sub-pentagonal; ambulacra short with blunt rounded tips, meet centrally over mouth in pentameral symmetry (no obvious 2–1–2 pattern); oral area small, apparently with three primary cover plates; spines poorly preserved, attached to upper cover plate surfaces, apparently single spine per cover plate, no obvious spine bosses preserved, spines long, approximately 1.3 mm in largest partial example; hydropore with single large, extremely thick plate larger posterior to and bordering adradial suture line of proximal part of ambulacrum V, transverse striations preserved in weathered specimens, particularly paratype PE 52708, hydropore slit bordered by four cover plates of ambulacrum IV; ambulacral cover plates arranged in single alternating biseries, perradial suture forming narrow zigzag pattern, cover plates erect, slab-like, much wider than long, thick, approximately twice as high as wide, with club-shaped, flat-topped, vertical extensions, slightly constricted medially, lower portion expanded transversely in both abradial and adradial directions, sutural passageways apparently opening below plate tops along sides of projecting ambulacra, cover plates mutually articulate adradially across floor of ambulacral groove along short flat sutures, each cover plate articulates abradially with hood plates, ambulacral tunnel tall, narrow; hood plates articulate along abradial mar-

gins of cover plates, elongate, medially constricted, hollow, apparently housing suspensory structures; interambulacral areas small, triangular, each with several thin squamose plates, seven or eight plates between ambulacral tips, merging distally into pedunculate zone plates; periproct large, conical, projecting well above thecal surface, of approximately 20 elongate lath-shaped plates; pedunculate zone of 23–30 rows of thin, wide, squamose, highly imbricate plates, obscuring and covering peripheral rim in contracted paratype PE 52717, peripheral rim best exposed in holotype, low (slightly inclined proximally) narrow peripheral rim, composed of three or four (?) imbricating circlets of tiny plates, proximal circlet not differentiated or enlarged.

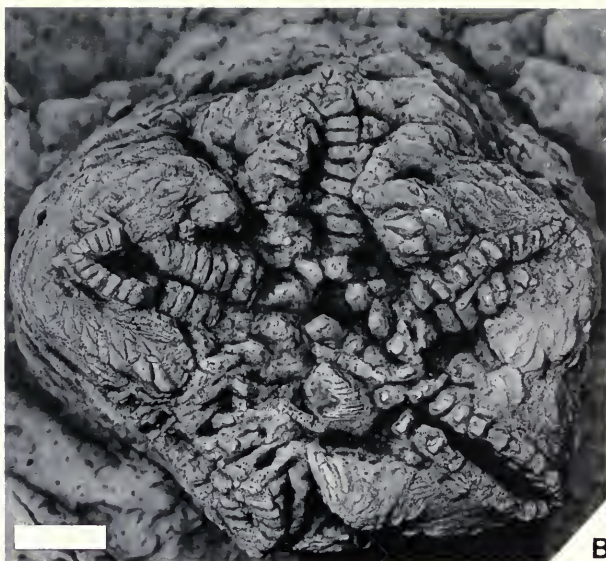
OCCURRENCE—Ten specimens were available for study, all but two collected by Guensburg. The holotype and seven paratypes all remain attached to original sites; two to poorly preserved nautiloid steinkerns, one to a fragment of trilobite exuvae, and one to an intraclast in a hardground; other paratypes are attached to indeterminate surfaces on a light brownish gray wackestone with numerous trilobite fragments and a few graptolites. All but one specimen were found on or near a thin limestone bed in a predominantly shaly interval of the *Calathium* calcisiltite member, Fillmore Formation, 23 m below the top of the Fillmore, trilobite zone I; paratype PE 52717 was found approximately 34 m below the top of the Fillmore in a more limestone-rich interval also in the *Calathium* calcisiltite member. Both occurrences are Upper Ibexian (Middle Arenigian), Early Ordovician in age. All specimens were collected near measured section H (Hintze, 1973) in the NW SW

FIG. 11. *Archaeopyrgus anitae*, n. gen. and sp. A, Holotype PE 52707, oblique view of partly extended specimen. Peripheral rim is attached to cephalopod steinkern. Scale bar = 2 mm. B, Paratype PE 52708, large, vertically crushed specimen. Scale bar = 2 mm. C, Paratype PE 52710, partly disrupted specimen showing many features of thecal interior. Scale bar = 1 mm. D, F, Paratype PE 52717, poorly preserved contracted specimen. D, Entire specimen attached to hardground; compare with reconstruction in Figure 15. Scale bar = 2 mm. F, End of much weathered ambulacrum showing cover plates that meet adradially. Scale bar = 0.5 mm. E, Paratype PE 52712, complete specimen left largely unprepared to show spines (faint) in matrix. Scale bar = 2 mm. (page 30)

FIG. 12. A, B, *Archaeopyrgus anitae*, n. gen. and sp. A, Holotype PE 52707, oral surface showing large hydropore oral (upper center) and periproct above. Well-preserved ambulacrum at left is drawn in Figure 13A. Scale bar = 1 mm. B, Paratype 52710, disrupted specimen showing interior of one side of an ambulacrum at left, cover plate extensions broken. Ambulacrum is drawn in Figure 13B. Scale bar = 1 mm. C, D, *Pyrgocystis* sp., referred specimen 1221TX30, Bromide Formation (Middle Ordovician) of Oklahoma. C, Specimen with spines partly removed showing short, strongly petalloid ambulacra. Scale bar = 1 mm. D, Enlarged oral view immersed in water showing sutural pores between cover plates. Scale bar = 0.5 mm. (page 31)



A



B



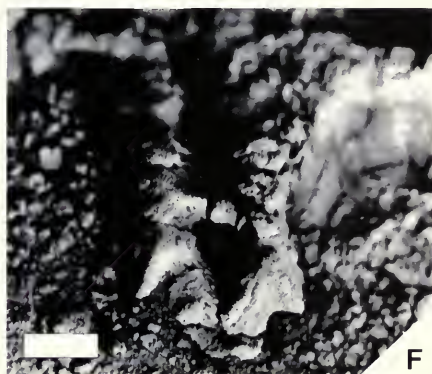
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D



E



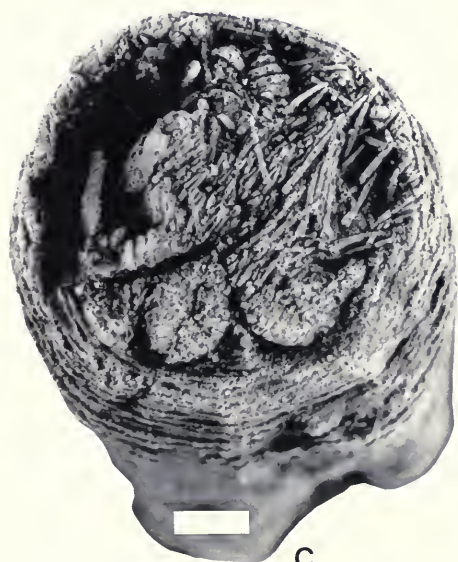
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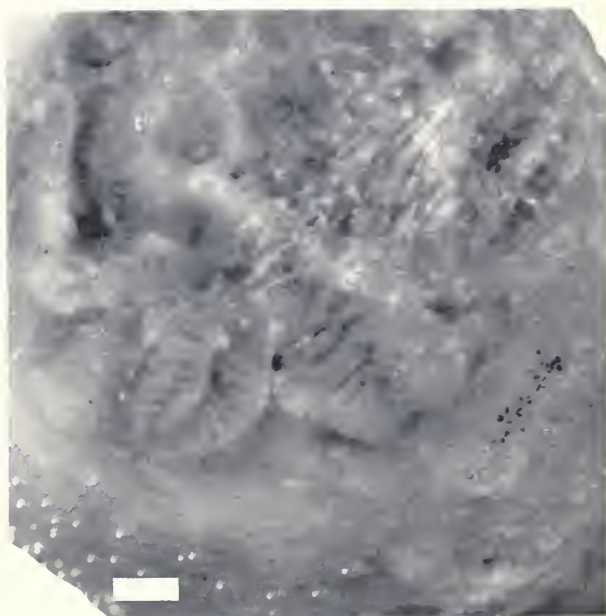
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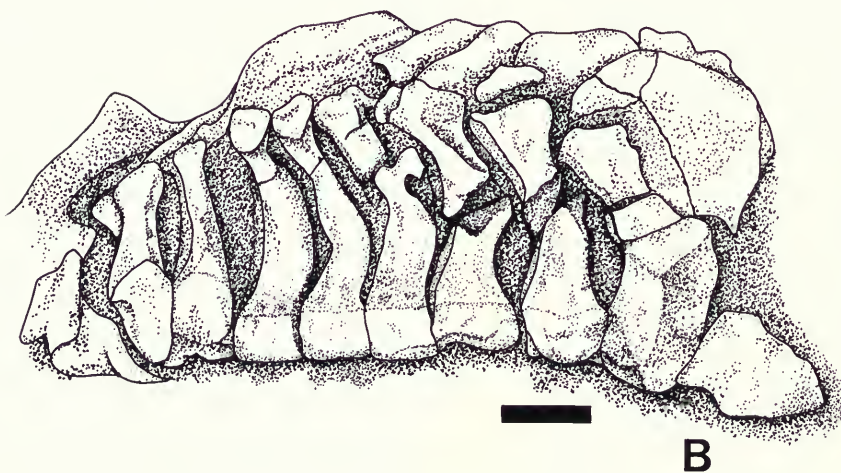
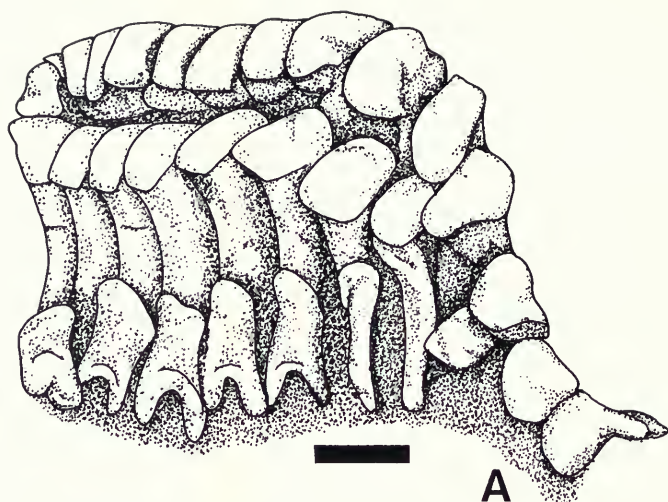


FIG. 13. Ambulacral morphology of *Archaeopyrgus anitae*, n. gen. and sp. Scale bar = 1 mm. A, Holotype PE 52707, oblique view of C ambulacrum. Note erect ambulacral cover plates and articulating lateral hood plates. B, Paratype PE 52710, interior view of ambulacrum showing cover plates, flat perradial articular facets with faint ligament pits above, followed by concave cover plate extensions with club-shaped summits. Note gaps between extensions forming cover plate passageways.

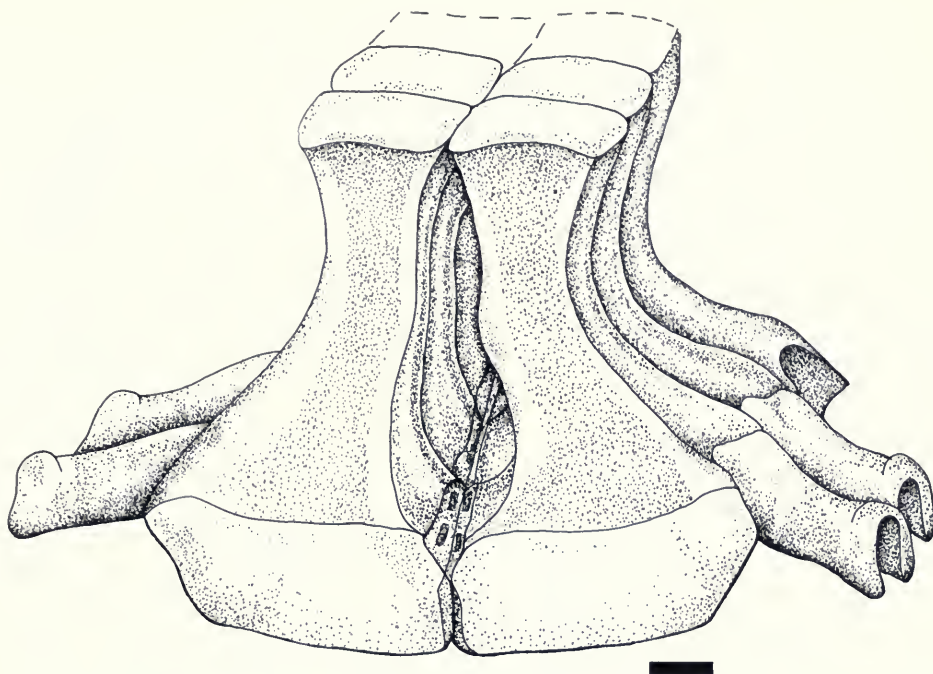


FIG. 14. Reconstructed ambulacral segment of *Archaeopyrgus anitae*, n. gen. and sp., in oblique view, primarily based on holotype PE 52707 and paratype PE 52710. Note shape of ambulacral tunnel and relationship of hood plates to cover plates. Scale bar = 0.5 mm.

NE, sec. 6, T23S, R14W, southwestern Ibex area in the southern Confusion Range, Millard Co., western Utah, USA.

SPECIMENS STUDIED—The holotype is PE 52707, and nine paratypes are PE 52708–52717.

ETYMOLOGY—Named for Anita Brosius of Cleveland, Ohio, for her assistance and good cheer in the field.

DISCUSSION—See Discussion under Genus *Archaeopyrgus*.

Genus *Fanulodiscus*

Guensburg and Sprinkle, new genus

TYPE SPECIES—*Fanulodiscus crystalensis* Guensburg and Sprinkle, new species.

DIAGNOSIS—Pyrgocystinid with small domal theca, ambulacra short, nearly straight-sided, not extending to peripheral rim, periproct small, cone-

shaped with lath-shaped plates, well-differentiated wide peripheral rim.

OCCURRENCE—Middle Ordovician, Utah, USA.

ETYMOLOGY—*Fanulo* from Latin meaning little temple, in reference to the flat-topped projecting ambulacra, and *diskos* from Greek meaning disc, for the general thecal shape.

DISCUSSION—*Fanulodiscus* is assigned to the pyrgocystinids based on the following characteristics: short petaloid ambulacra, small oral area, thick slab-like flat-topped cover plates, and the presence of lateral hood plates. The holotype of *Fanulodiscus* shows well the nature of the oral plating and the original positioning of the lateral hood plates. Virtually nothing is known of the interior construction. The obvious difference of *Fanulodiscus* from traditional pyrgocystinids is the lack of a pedunculate zone. The only other domal edrioasteroid that we assign to the pyrgocystinids is *Epipaston* Holloway and Jell, 1983, from the Silurian of Australia. This genus can readily be distinguished from *Fanulodiscus* by its wider, con-

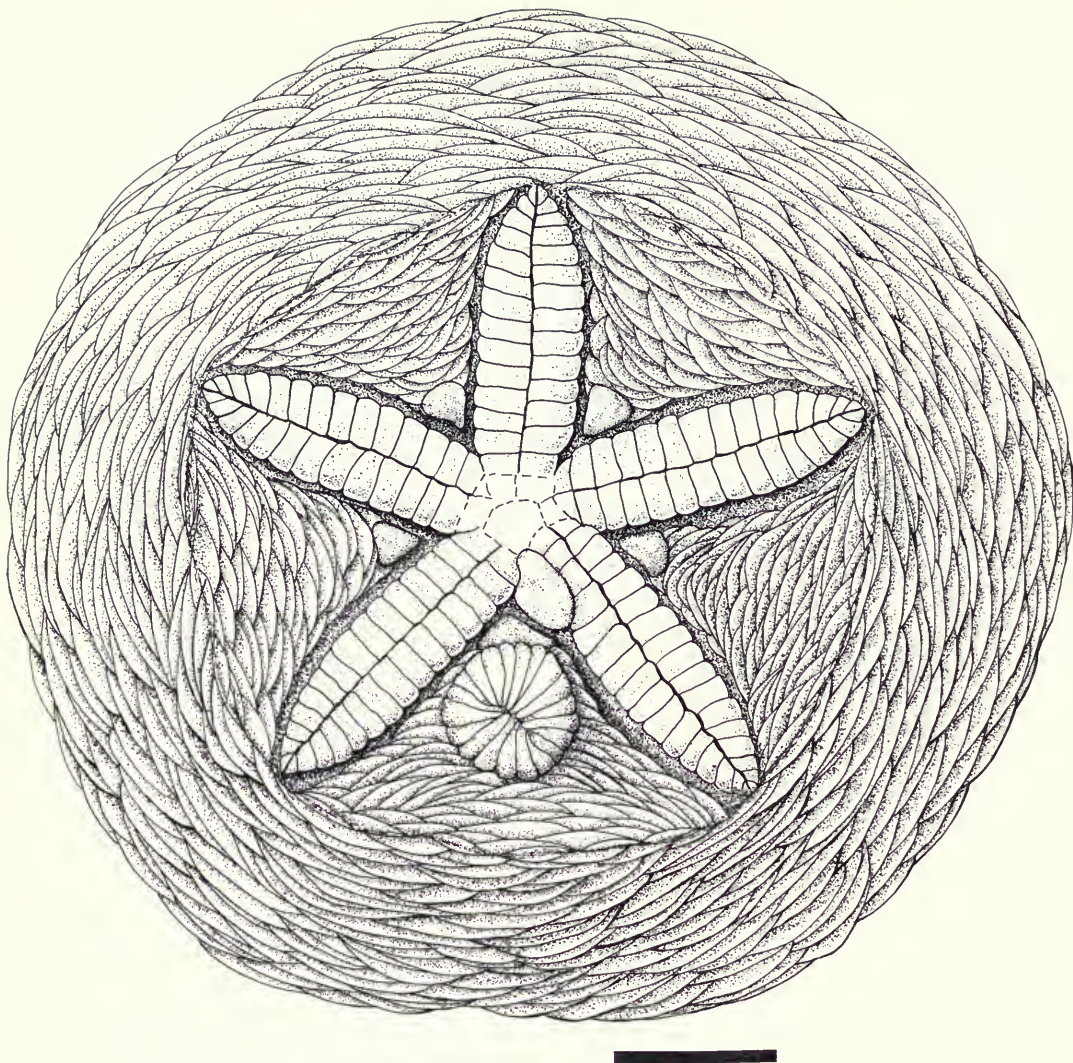


FIG. 15. Reconstructed oral view of *Archaeopyrgus anitae*, n. gen. and sp., with theca contracted, based primarily on paratype PE 52717. Plating at center of oral area is poorly known and indicated with dashed lines. Darkened depressed areas adjacent to ambulacra mark positions of hood plates that are largely obscured in this orientation. Scale bar = 2 mm.

vex-sided petalloid ambulacra and heavy spines on the proximal circlet of the peripheral rim.

***Fanulodiscus crystalensis*,
new species**

Figures 17A, B, 18

DIAGNOSIS—Same as that of genus.

MATERIAL AND DESCRIPTION—The four speci-

mens available occur on a small slab, and only the holotype preserves detail of the ambulacra, oral area, and periproct; theca small, diameter ranging from 7 to 10 mm, averaging 7.9 mm, theca probably highly domal with projecting ambulacra in life but now collapsed; ambulacra five, petalloid, short, relatively narrow, straight-sided, with blunt tips; oral area small, with three primary oral cover plates, posterior primary oral largest; hydropore oral, situated in proximal posterior interambulacrum, thick, massive, with adradial plate margin

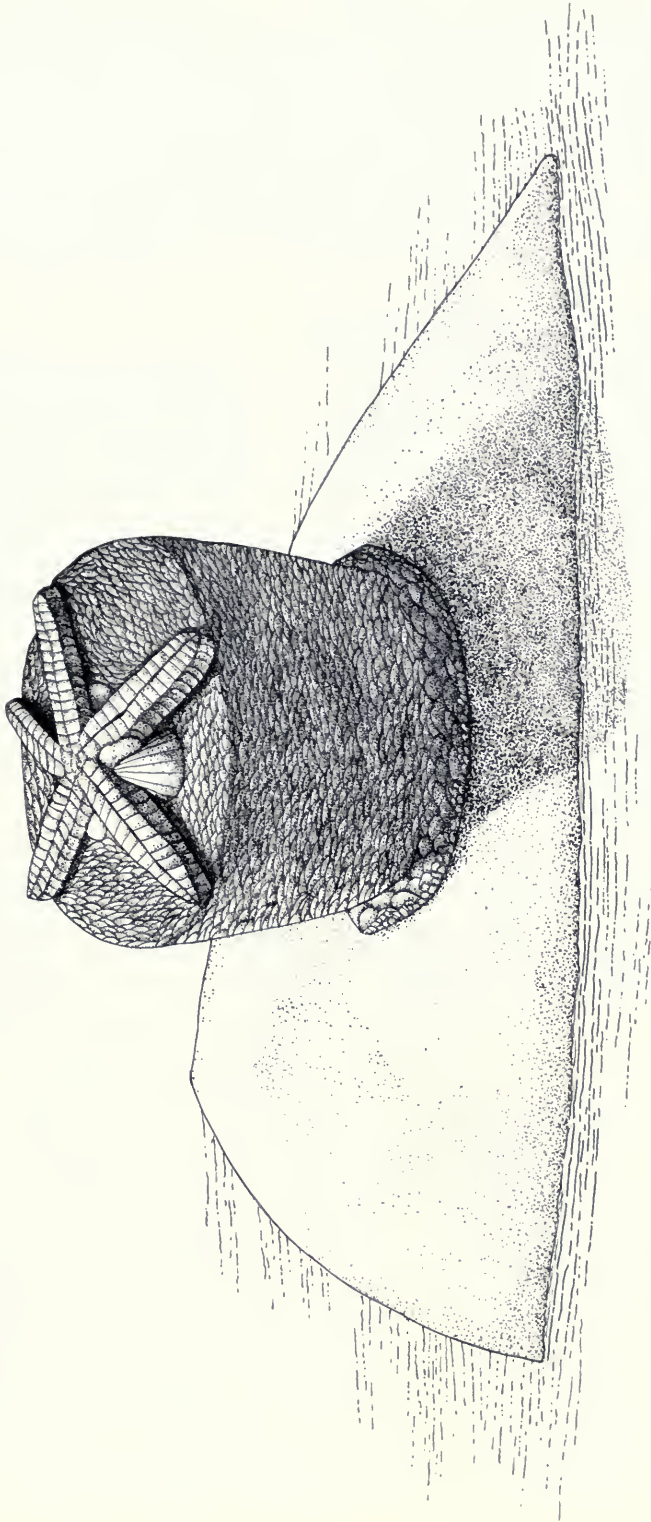
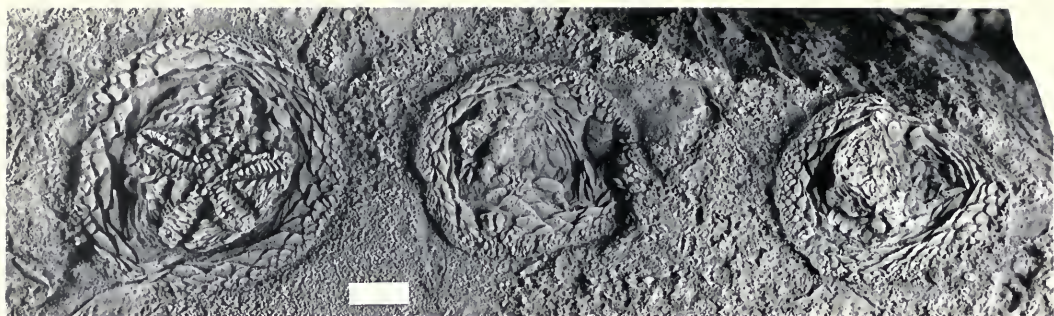
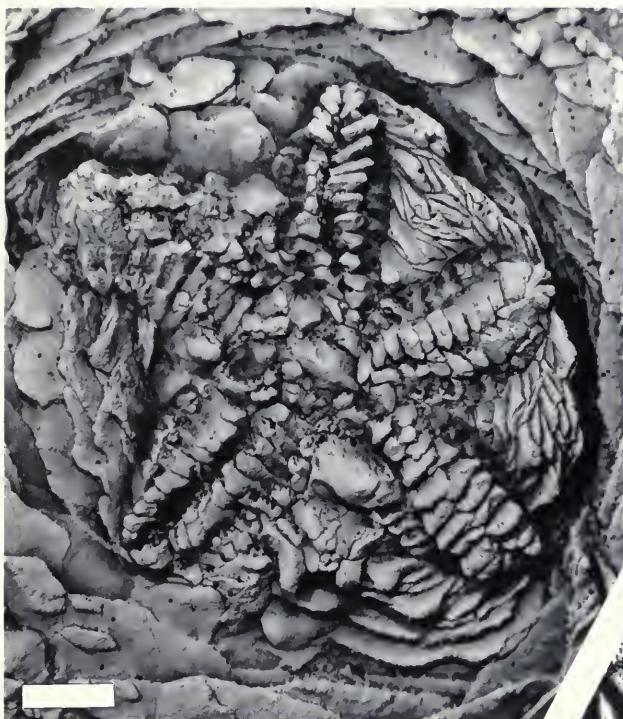


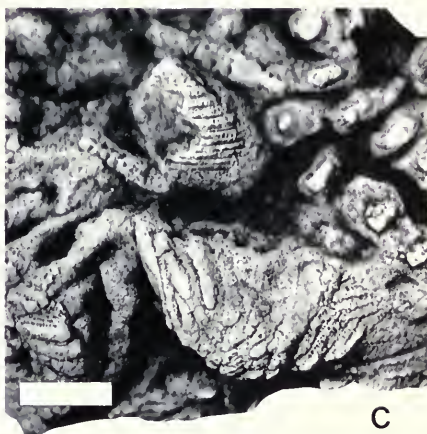
FIG. 16. Reconstruction (much enlarged) of *Archaeopyrgus anitae*, n. gen. and sp., shown in extended position and attached to a partly buried fragment of a nautiloid conch. Central oral plating is conjectural and cover plate spines were omitted because they are poorly known.



A



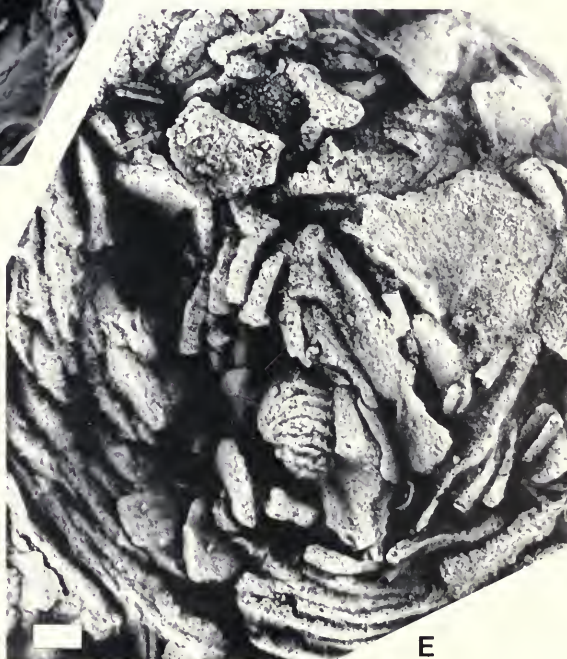
B



C



D



E

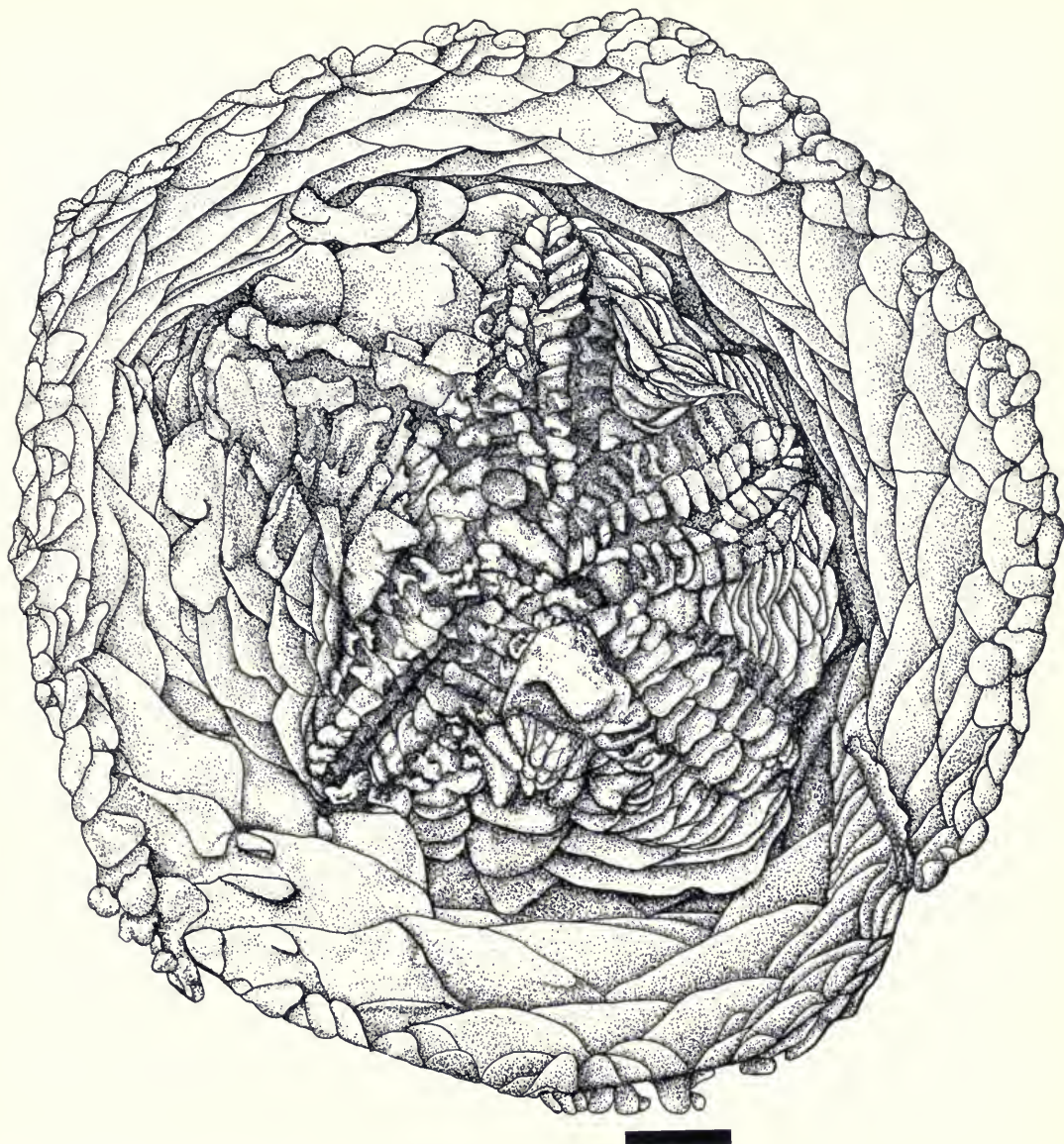


FIG. 18. Oral surface of *Fanulodiscus crystalensis*, n. gen. and sp., holotype USNM 172048. Lateral hood plates are visible beside cover plates. Scale bar = 1 mm.

←

FIG. 17. **A, B**, *Fanulodiscus crystalensis*, n. gen. and sp. **A**, Holotype USNM 172048 (left) and paratypes USNM 172049–172050 attached to hardground. Scale bar = 2 mm. **B**, Holotype. Note well-preserved oral surface with slab-like cover plates, lateral hood plates, and large hydropore oral plate. Drawing of this specimen appears in Figure 18. Scale bar = 1 mm. **C**, *Archaeopyrgus anitae*, n. gen. and sp., paratype PE 52708, hydropore oral with striations (above) and periproct (below). Scale bar = 1 mm. **D**, *Cyathocystis* sp., PE 52718, Kimmswick Limestone (Middle Ordovician) of Missouri. Cover plates are largely missing, revealing intrathecal passageways through deltoids. Scale bar = 1 mm. **E**, *Pyrgocystis* sp., referred specimen 1279TX333, Bromide Formation (Middle Ordovician) of Oklahoma, disarticulated, showing hydropore oral with striations (lower center). Scale bar = 0.5 mm.

contacting cover plates proximal ambulacrum V; ambulacral cover plates forming simple alternating biseries, narrow zigzag perradial suture; cover plates thick, slab-like, with club-like external projections, upper surfaces flattened, lateral abradial margins nearly vertical; single hood plate abradial to and articulating with adjacent cover plate, highly convex and medially constricted, apparently housing suspensory structures, gaps between hood plates at medial constrictions apparently communicate with thecal interior; interambulacral areas small, of 10–13 plate rows, interambulacral plates small, thin, imbricate, except for adoral-most plate, which is thick, with single central node; interambulacrals continue distally from ambulacra in series of highly squamose plates and form short extensible thecal elongation zone; peripheral rim large, prominent in collapsed fossils, of five to six imbricate plate circlets, proximal circlet grading into distalmost interambulacrals.

OCCURRENCE—The four small specimens are attached to a small slab of intraformational conglomerate that was apparently also a hardground. No other attached fossils are represented. The edrioasteroids were collected by Lehi Hintze and associates along the Crystal Peak measured section (Hintze, 1973) approximately 11 m above the base of the Lehman Formation, Lower Whiterockian Stage (Llanvirnian), Lower Middle Ordovician. The collecting locality is in the SE NW, sec. 24, T23N, R16W, southwestern Ibex area in the southern Confusion Range, Millard Co., western Utah, USA.

SPECIMENS STUDIED—The holotype is USNM 172048, and the three associated paratypes are USNM 172049–172051.

ETYMOLOGY—Named for Crystal Peak, a prominent landmark just south of the collecting locality.

DISCUSSION—See Discussion under Genus *Fanulodiscus*.

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Appendix

Following is a compilation of edrioasteroid genera placed in our classification scheme, expanded and modified from Bell (1980). The agelacrinitids are easily the most diverse of edrioasteroid families; several subfamilies are likely present, but these are not treated here, pending revision of the group. Limitations of time prevented a complete literature search, and the list is not exhaustive.

Class EDRIOASTEROIDEA Billings, 1858

Order CAMPTOSTROMATOIDA Durham, 1966

Family CAMPTOSTROMATIDAE Durham, 1968

Camptostroma Ruedemann, 1933

Order STROMATOCYSTITIDA Bell, 1980

Family STROMATOCYSTITIDAE Bassler, 1935

Stromatocystites Pompeckj, 1896

Order and Family Uncertain

Cambraster Cabibel, Termier, and Termier, 1958

Walcottidiscus Bassler, 1935

Order ISOROPHIDA Bell, 1976

Family Uncertain

Edriodiscus Smith, 1985

“*Stromatocystites*” *walcotti* Schuchert, 1919

Family AGELACRINITIDAE Chapman, 1860

Agelacrinites Vanuxem, 1842

Cooperidiscus Bassler, 1935

Curviriordo Bell, 1976

Deltadiscus, n. gen.

Dinocystis Bather, 1898

Discocystis Gregory, 1897

Hadrochthus Bell, 1976

Hemicystites Hall, 1842

Hystrichopsydrax Guensburg, 1988

Isorophus Foerste, 1917

Isorophusella Bassler, 1935

Krama Bell, 1976

Lepidodiscus Meek and Worthen, 1868

Lispidecodus Kesling, 1967

Neoisorophusella Kammer, Tissue and Wilson, 1987

Postibulla Bell, 1976

Rectitriordo Bell, 1976

Savagella Foerste, 1920

Spiraclavus Sumrall, 1992

Stalticodiscus Smith, 1983

Thresherodiscus Foerste, 1914

Timeischytes Ehlers and Kesling, 1958

Ulrichidiscus Bassler, 1935

Family LEBETODISCIDAE Bell, 1976

Subfamily LEBETODISCINAE Bell, 1976

Argodiscus Prokop, 1965

Belochthos Bell, 1976

Chatsworthia Smith and Jell, 1990

Cystaster Hall, 1871

Euhydrodiskos Guensburg, 1988

Floridiscus Smith, 1980

Foerstediscus Bassler, 1935

Hadrodiscus Smith and Jell, 1990

Lebetodiscus Bather, 1908

Streptaster Hall, 1872

Subfamily CARNEYELLINAE Bell, 1976

Carneyella Foerste, 1917

Cryptogoleus Bell, 1976

Subfamily PYRGOCYSTINAE Kesling, 1967

Archaepyrgus, n. gen.

Epipaston Holloway and Jell, 1983

Fanulodiscus, n. gen.

Pyrgocystis Bather, 1915

Order EDRIOASTERIDA Bell, 1976

Suborder EDRIOASTERINA Bather, 1898

Family TOTIGLOBIDAE Bell and Sprinkle, 1978

Totiglobus Bell and Sprinkle, 1978

“*Totiglobus*” *lloydi* Sprinkle, 1985

Family EDRIOASTERIDAE Bather, 1898

Edrioaster Billings, 1858

Edriophus Bell, 1976

Paredriophus, n. gen.

Suborder EDRIOBLASTOIDINA Fay, 1962

Family ASTROCYSTITIDAE Bassler, 1935

Astrocystites Whiteaves, 1897

Cambroblastus Smith and Jell, 1990

Lampteroblastus, n. gen.

Family CYATHOCYSTIDAE Bather, 1899

Subfamily CYATHOCYSTINAE Bather,
1899

Cyathocystis Schmidt, 1879

Subfamily RHENOPYRGINAE Hollo-
way and Jell, 1983

Rhenopyrgus Dehm, 1961

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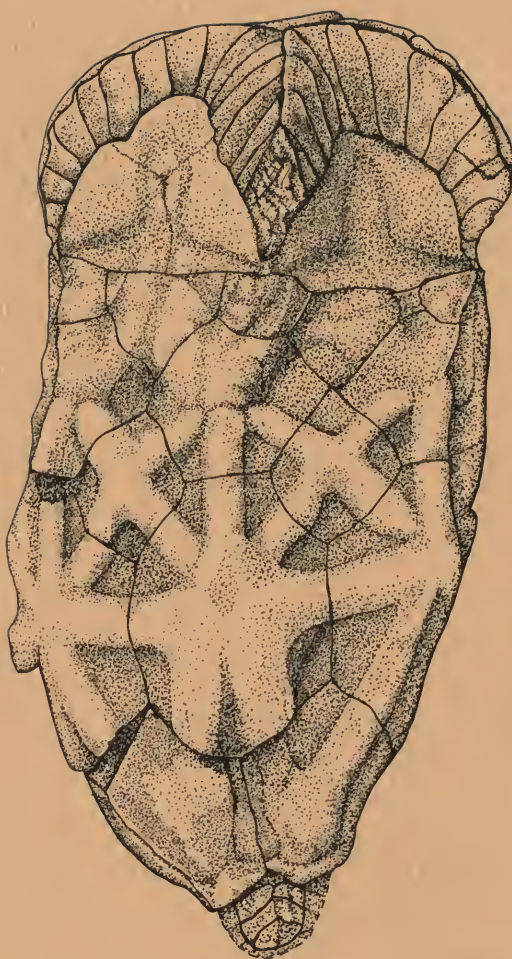
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